



MADROÑO

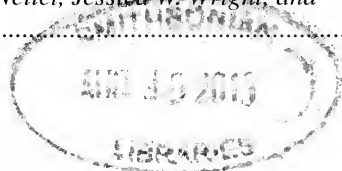
A WEST AMERICAN JOURNAL OF BOTANY

CENTENNIAL YEAR 1913–2013

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MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbaria, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription information on inside back cover. Established 1916. Periodicals postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to MADROÑO, Kim Kersh, Membership Chair, University and Jepson Herbarium, University of California, Berkeley, CA 94720-2465. kersh@berkeley.edu.

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TANOAK: HISTORY, ECOLOGY AND VALUES

FOREWORD

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Key Words: Acorns, *Lithocarpus densiflorus*, *Notholithocarpus densiflorus*, *Phytophthora ramorum*, sudden oak death, tanoak.

To combat sudden oak death (SOD), scientists needed to understand its primary host – tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), so research was initiated on its distribution, utilization and natural history. This *Madroño* Special Issue presents much of what we have learned, over the past 10 years, about this endemic, broadleaf tree, common throughout coastal California and southwest Oregon. By assembling this work, we aim to synthesize new information about this important SOD host; apply the concepts and findings to conservation and management; and share our appreciation for tanoak.

The articles in this issue, on tanoak ecology, population genetics, and associated organisms, can only begin to hint at the significance of this California native tree. Lamentably, tanoaks' character has become more apparent from viewing its demise. Since the mid-1990s, millions of tanoak trees have been lost to the exotic pathogen, *Phytophthora ramorum*, the causative agent of SOD. The cliché, "You don't know what you have until it's gone" has played out in backyards, parks, forests, wilderness areas, and along roadsides from Monterey County northward into Curry County, Oregon. Where tanoak once resided, we have come to more fully appreciate the "sovereign oak", for lost along with the groves are beauty, ambience, habitat,

food, soil stability, screening and other less tangible values.

Society has had profound impacts on the tanoak ecology, and its current status reveals much about human culture and relationship to nature. Over the past century tanoak has been adored and despised: prized for its acorns; debarked for tannins; treated with herbicides to reduce competition for commercial conifers; and coveted as part of the urban forest. Tanoaks are tenacious and vulnerable: they sprout vigorously, but are very susceptible to SOD. Conservation of the tanoak resource is a challenge that requires consideration of botany, ecology, forestry and the conflicting values of diverse populations, all of which are confounded by an emerging exotic pathogen. We invite your collaboration in our aspiration to care for tanoak.

Many of the papers in this issue were presented orally at "Tanoak Wild: A Celebration" held June 22, 2012 in Petaluma, CA, as part of the Fifth Sudden Oak Death Science Symposium. Thanks to the authors and to the more than 25 reviewers. We appreciate the assistance of Laura Lee George, Melodie K. George-Moore, Suellen Ocean, Ian Pearse, Beth Purcille, Lois Risling, Matt Ritter, and Ralph Shanks. Funding for this issue was provided by the USDA Forest Service, Pacific Southwest Research Station, and the California Botanical Society.

TANOAK LANDSCAPES: TENDING A NATIVE AMERICAN NUT TREE

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ABSTRACT

Notholithocarpus densiflorus (Hook. & Arn.) Manos, Cannon & S.H. Oh (Fagaceae) (tanoak) needs immediate conservation attention due to the threat posed by *Phytophthora ramorum* Werres, de Cock & Man in't Veld, the water mold responsible for sudden oak death. This article explains the significant cultural value of tanoak and the seriousness of the sudden oak death threat. Current efforts to limit the spread of *P. ramorum* are not working adequately to prevent pathogen spread and maintain healthy ecosystems. The heartland of tanoak's distribution in northern California is at risk. I advocate for a collaborative process with tribal leadership to identify areas with mature tanoaks where traditional indigenous burning practices can be tested in combination with best management practices informed by western science. New approaches are needed to tend to tanoaks despite the sudden oak death pathogen and other threats.

Key Words: *Lithocarpus densiflorus*, *Notholithocarpus densiflorus*, tanoak, traditional ecological knowledge.

A century ago a non-native disease inadvertently introduced on an infected garden plant began to spread in North America's eastern deciduous forests. Within decades the once widespread American chestnuts (*Castanea dentata* [Marshall] Borkh.) succumbed to chestnut blight and no longer produced nutritious nuts for people, livestock, and wildlife in most of its native range (Freinkel 2007). Today, a similar fate may await a West Coast native nut tree: tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh. Since the horticultural trade accidentally introduced the sudden oak death (SOD) pathogen to North America, over a million tanoaks have died (Meentemeyer et al. 2011), and an unknown number are infected. The disease was first detected in California in the mid-1990s (McPherson et al. 2005; Kluza et al. 2007), and it continues to spread despite the efforts of landowners, scientists, and government agencies. Currently no cure exists for infected trees, and thus far tanoak exhibits little genetic resistance to the exotic water mold that causes the disease: *Phytophthora ramorum* Werres, de Cock & Man in't Veld (Hayden et al. 2011). Computer models rank uninfected areas on the north coast of California as high risk for infection (Meentemeyer et al. 2004; Kliejunas 2010).

Tanoak deserves more conservation attention due to its cultural and ecological importance. This magnificent tree, along with its relative American chestnut, reminds us that even common plants can rapidly become threatened. Fortunately large areas with extensive tanoak stands remain uninfected. The southern-most populations near Santa Barbara and inland populations away from the coast are probably too dry to foster SOD. However, because “an

alarming number of uninfected forest ecosystems ... face considerable risk of infection” plant pathologists recommend “that we develop effective management strategies for susceptible forests and that we prevent long distance spread of the pathogen, a threat that could drastically alter forests in California” (Meentemeyer et al. 2004).

THE BEAUTIFUL TREE

In the Kashaya Pomo language, tanoak is called *chishkale*, which translates to “beautiful tree” (Gifford 1967). In 1889, the first botany professor at the University of California at Berkeley, Edward L. Greene, called tanoak “the most remarkable of all North American oaks” and listed it as being “among the most beautiful of Californian forest trees” (Greene 1889). Generally a medium sized tree, its height typically ranges from “15.2 to 27.4 m” with a maximum height recorded at 63.4 m (Tappeiner et al. 1990). Diameter at breast height in mature trees ranges from “15 to 122 cm” and “the largest diameter of record is 277 cm” (Tappeiner et al. 1990). The overall shape of this evergreen tree varies greatly depending on growing conditions. However, two common forms exist, one that grows in full sun and another in dense shade. In open stands dominated by hardwoods, tanoaks form a broad, dense crown and a short trunk with robust horizontal branches. In shady, dense coniferous forests, tanoaks often grow as tall as 45.7 m with a branchless trunk that is “clear for 9.1 to 24.4 m” (Tappeiner et al. 1990). Taller trees with long trunks growing with coniferous competition lend themselves to wood production while the trees grown in sunny exposures generate a greater abundance of food in the form of acorns (Fig. 1).



FIG. 1. Tanoak in open prairie with robust canopy, a legacy of frequent, low-intensity fires set by Native people. Ukiah, California, circa 1903. Photograph by A. O. Carpenter (Plate 7 in Jepson 1910). Image courtesy of the University and Jepson Herbaria Archives, University of California, Berkeley.

As is typical for members of the Beech Family (Fagaceae), tanoak has unisexual flowers. The tree can flower during any season except winter, but typically blossoms appear in June, July, or August with coastal and low-elevation trees blooming earliest (Roy 1957b). The small, solitary female flowers aggregate at the base of the erect male catkin, each subtended by a small bract (Fig. 2). The abundant yellowish-white male spikes “light up the tree like candles at Christmas” (Fig. 3) (Peattie 1991). Drought during pollination fosters greater seed set (Tappeiner et al. 1990). Once pollinated via wind or insects, acorns mature after two years. Tanoak’s simple leaves alternate on the stem. Notorious for being highly variable, the leaves are “leathery to brittle” with serrated to toothless edges and often revolute margins (Nixon 1997). The usually smooth and shiny leaves are densely wooly beneath initially but much of the hair wears off with age. The thick, grayish-brown bark becomes fissured with age. Tanoaks are often difficult to reliably age due to heart rot and the high frequency of suckering if killed to the ground. Its hard wood also makes coring a tanoak trunk to count growth rings quite challenging. However, throughout its range, 180 years appears to be a typical maximum age in unlogged forests, with estimates reaching as high as 300–400 yrs (Fryer 2008).

Tanoak trees grow from southwestern Oregon through the California Coast Range to near Santa Barbara, with inland populations occurring through the Siskiyou Mountains and from the southern tip of the Cascade Range along the western slopes of the Sierra Nevada to Yosemite National Park (Tappeiner et al. 1990; Tucker 2012). The shrub variety, *Notholithocarpus densiflorus* var. *echinoides*, (R. Br.) Manos, Cannon & S. H. Oh extends from southwestern Oregon to northern California’s Klamath Range, Cascade Range, and Sierra Nevada. A mutant, shrub-like form grows in Yuba County in the northern Sierra Nevada (forma ‘*attenuato-dentatus*’) (Tucker et al. 1969). This mutant is used in horticulture due in part to its rarity. It has a maximum height of roughly 2.4 m. and unusual, deeply serrated, narrow leaves, each with a very narrow apical tip. No other taxa belonging to this genus exist on the planet. A prominent U.C. Berkeley botany professor, Willis Linn Jepson, wrote in 1910 that tanoak is “exceptionally well-fitted by its reproductive powers, vigor and shade endurance to take part in the struggle for continuous possession of the land”—hence its other common name, sovereign oak (Jepson 1910).

EARLY INDIGENOUS PEOPLES’ USE OF TANOAK

Tanoak acorns formed the basis of a California Indian acorn economy for thousands of years (Fig. 4). Today they remain a highly valued food among indigenous tribal peoples. In northern California, at least after American settlement, salmon was the only other food consumed in larger quantities. Though indigenous peoples gathered and favored acorns from multiple oak species, northwestern tribes in particular often preferred tanoak when obtainable (Gifford 1971; Chestnut 1974; Heizer and Elsasser 1980). E. W. Gifford, an academic expert on acorn eating or balanophagy in California, ranked tanoak number one in popularity and black oak (*Quercus kelloggii* Newb.) second (Gifford 1971). Although controversial, anthropologist Martin Baumhoff defended rating as important “because in many areas people would travel a long way to a single tree of a preferred species while ignoring nearby groves of an undesirable species” (Baumhoff 1978). Three remnant Tolowa tanoak groves totaling roughly 500 mature trees along the Smith River were estimated to annually produce “14.4 tons ... of usable food materials when dried” (Gould 1976).

In addition to serving as a staple food, tanoak was used in the making of fishing nets, baskets, and medicines. The Tolowa used tanoak bark to dye their nets in order to make them less visible to fish (Baker 1981). Since tannins have a history of being used to preserve fibers such as cloth sails for ships as well as fishnets, the Tolowa may have gained longer use of their nets (Schniewind 1958).

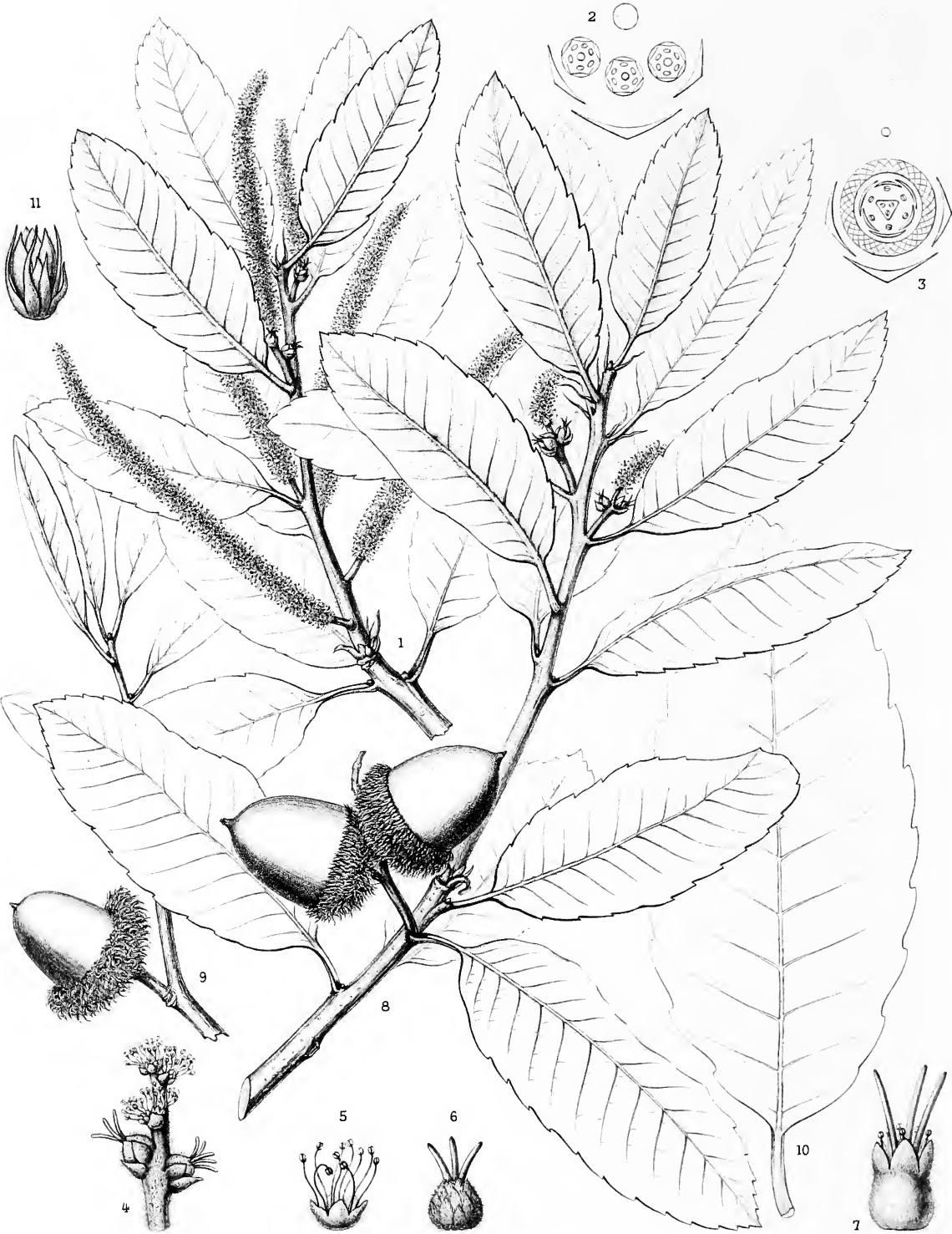


FIG. 2. Tanoak twig with female flowers, male flowers, male catkins, and acorns. Illustration by Charles Edward Faxon (Tab. CCCCXXXVIII in Sargent 1895).

The Costanoan/Ohlone also prepared a dye from tanoak bark (Bocek 1984). Oak saplings including tanoak were used in heavy-duty baskets. In baby baskets tanoak served to protect the

infant's head. The oak rim of hopper baskets used during acorn pounding needed to be strong because women rested their legs on it to hold it in place around the mortar (S. Smith-Ferri, Grace Hudson



FIG. 3. Tanoak portrayed in Curtis’s botanical magazine (Tab. 8695 in Prain 1917).

Museum, personal communication, 14 September 2011). Among the Kashaya Pomo, tanoak acorns functioned as cough drops as the tannins suppressed coughing (Goodrich et al. 1980). The Costanoan/

Ohlone used a tanbark decoction to treat facial sores and loose teeth (Bocek 1984). Tanoak was so highly regarded by the Sinkyone that “[d]reams of tanoak ... were a sign of good luck” (Nomland 1935).

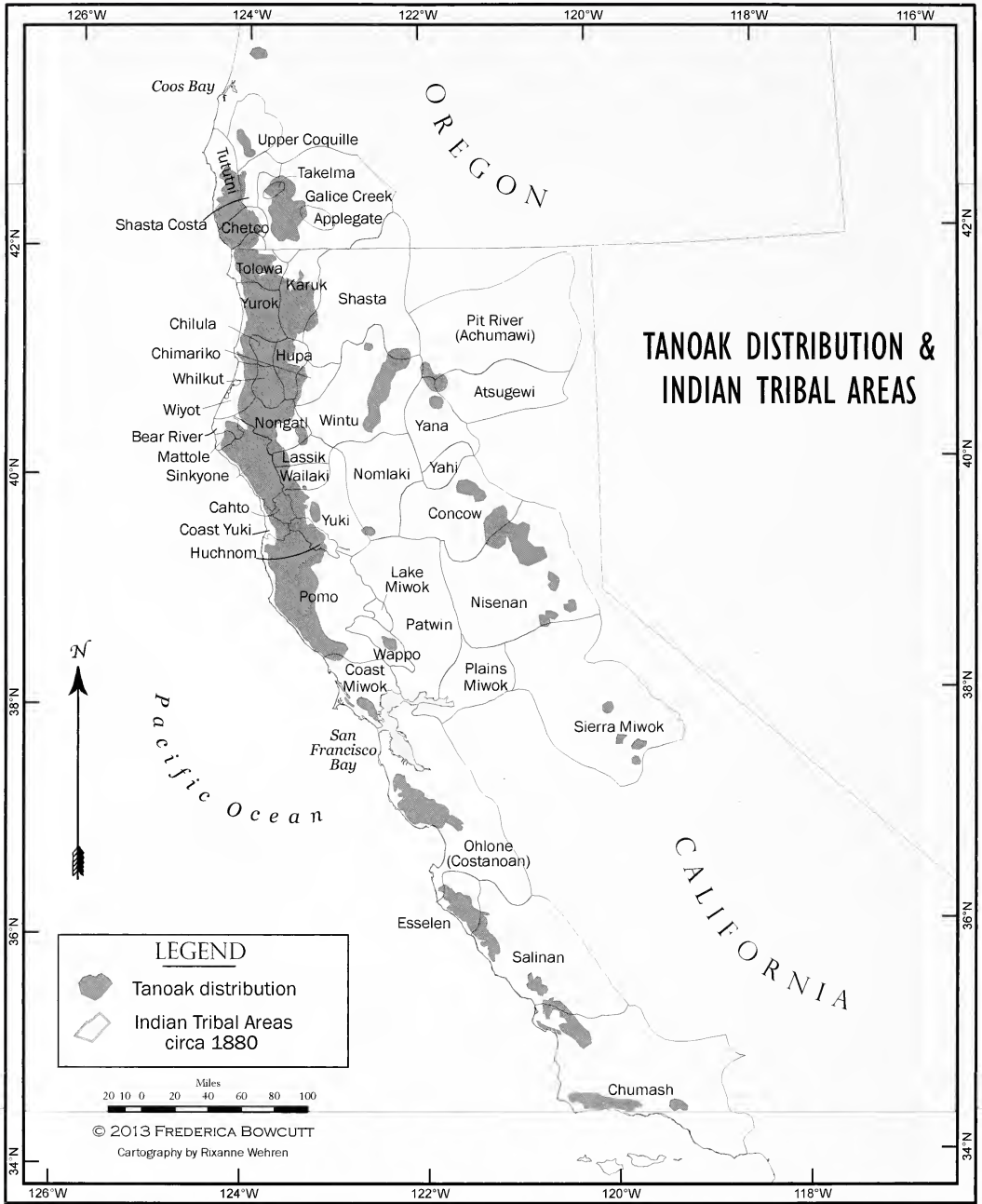


FIG. 4. Tribal territorial map and tanoak distribution. Data sources: M. Kat Anderson, USDA-NRCS, provided the tribal boundaries digital map layer for California. Minor adjustments were made based on data provided by Jerry Rohde, Cultural Resources Facility at Humboldt State University; Hawk Rosales, executive director of the InterTribal Sinkyone Wilderness Council, and the American Philosophical Society (2012). The tribal boundaries for Oregon were derived primarily from Schaeffer (1959). The tanoak distribution data for California came from Griffin and Critchfield (1976). Tanoak distribution data for Oregon came from the Oregon Flora Project (2012).

Multiple characteristics of the acorns contribute to tanoak's popularity as a staple food among many California Indian tribes. A thicker shell makes the delicious nut more resistant to fungal and insect attacks (Wolf 1945; Heizer and Elsasser 1980). Tanoak acorns store for years, making them a desirable trade item. For example, the Karuk (or Karok) swapped tanoak acorns for "white deer skins, obsidian, dentalia shells, and Sugar Pine nuts" with Shasta people (Davis 1991). Relative to other oaks, tanoak is one of the more reliable producers, rarely failing completely and bearing bumper crops more frequently. Tanoaks "are heavily laden almost every

alternate year and complete seed crop failures are rare,” helping to give it the reputation of being the heaviest acorn producer of all Pacific Coast oak species (Roy 1962). Annual nut production in most other nut-bearing trees varies significantly with heavy crops every two to five yrs. The “non-mutually exclusive hypotheses” proposed for this masting behavior include, genetics, climatic conditions, and coevolution with seed eating animals to limit their population growth (Vander Wall 2001). Tanoak trees typically begin to bear an abundance of acorns when they’ve reached between 30 and 40 yrs old, “although 5-year-old [root] sprouts also have produced fairly heavy crops” (Roy 1962). A mature tanoak tree bears more than 90 kg of nuts on average in a good year, with estimates as high as 454 kg annually for old growth trees (Radtke 1937; Baumhoff 1963). Each nut typically exceeds the size of a hazelnut.

Compared to grains like wheat, tanoak acorns are low in protein but superior in caloric value due to the high amount of nutritious fats they contain (Table 1) (Baumhoff 1963). Nutrition scientist Linda Ellen Gilliland completed a study in 1985 in which she found that protein and fat content varied significantly in acorns, but she corroborated that protein content is low and fat and carbohydrate content are moderately high in tanoak acorn foods. However, she did not analyze mineral content for tanoaks as suggested in the title of her thesis (Gilliland 1985). More research is needed on the nutritional value of tanoak acorns, because many other health-promoting constituents exist in plant foods other than fat, fiber, carbohydrate, and protein. Acorns are soft enough to chew without processing, but the tannic acid they contain must be removed to make them useful as human food (Essene 1942). Compared to most acorns, tanoak nutmeats are significantly larger, making them easier to process.

Tanoak-acorn harvesting occurred and continues to occur during autumn. Based on the ethnographic record, Karuk families gathered in October for roughly a month (Schenck and Gifford 1952). The Yuki collected tanoak acorns “far up in the mountains in November when they were ripe” at higher elevation (Curtin 1957).

Collecting often occurred some distance from winter residences. The Tolowa moved to the inland edge of the redwood belt for a month to gather nuts before moving back to coastal villages (Gould 1976). According to Pomo ethnographer Fred Kniffen, “no trip was too long to make for these highly desired nuts” (Kniffen 1939). Families picked up acorns under tanoak trees after they fell naturally. Some tribes used sticks to knock acorns down, although others believed this practice was harmful to the trees as it can cause nuts in their first year of development to fall, thus reducing the following year’s harvest. Pomo men climbed mature trees or, if smooth barked, they used “a sapling or a fallen redwood as a ladder” and then stamped “on the branches to shake” acorns down (Gifford 1967). Openwork burden baskets were used to transport the harvest (Shanks and Shanks 2006).

Annual first-acorn ceremonies preceded consumption of the nuts each autumn (Wallace 1978). Among the Sinkyone this ceremony lasted five nights (Nomland 1935). Mary Socktish, an officiate of the Hupa’s first acorn feast, recounted in 1940 the associated rituals. Typically, in early October or rarely in late September, she and several other women harvested the earliest ripe acorns. The night before the feast, she prayed for “plenty of acorns,” addressing her request to “the acorn ‘boss’—Yinukatsisdai, the god of vegetation.” Several other women assisted her in praying for a good harvest most of the night in the “sacred living house.” After bathing at three a.m. in the cold river, the women began to de-skin, winnow, pound, and sift the already shelled acorns. Around sunrise, the women took the acorn meal to the river for leaching and cooking at the feasting place. “While the stones are heating, we prepare fall salmon, broiling it on sticks around the fire. ... After the acorn meal is all cooked, about two o’clock in the afternoon, a messenger is sent to notify the people to come to the feast. The people come along a special trail.” Socktish warned: “Whoever wastes acorns at any time will not have plenty” (Kroeber and Gifford 1949).

Indigenous peoples developed food technologies for storing, processing, and cooking tanoak

TABLE 1. NUTRITIONAL COMPOSITION BY PERCENTAGES OF SELECT ACORNS COMPARED TO BARLEY AND WHEAT. Adapted from page 25 of Basgall (1987), and page 162 of Baumhoff (1963).

Species	Fats	Fiber	Carbohydrates	Protein
Black oak (<i>Quercus kelloggii</i>)	11.1–18	11.4	55.5	3.4–4.6
Blue oak (<i>Q. douglasii</i>)	4.8–8.1	9.8	65.5	3.0–5.5
Canyon oak (<i>Q. chrysolepis</i>)	8.7	12.7	63.5	4.1
Coast live oak (<i>Q. agrifolia</i>)	14.5–16.8	11.6	54.6	3.1–6.3
Oregon white oak (<i>Q. garryana</i>)	4.5	12	68.9	3.9
Valley oak (<i>Q. lobata</i>)	4.2–5.5	9.5	69	2.8–4.9
Tanoak (<i>Notholithocarpus densiflorus</i>)	12.1	20.1	54.4	2.9
Barley	1.9	5.7	71.0	8.7
Wheat	1.8	2.3	69.4	12.3

acorns to yield a sweet, nutty meal rich in complex carbohydrates and essential fatty acids. Storage inside homes helped to protect against rodents (Baumhoff 1963). Among the Lassik, all tanoak acorns were stored inside while other acorn types were stored outside at least in part indicating how valued tanoak acorns were (Essene 1942). Pomo women reduced spoilage by drying whole tanoak acorns in the sun before storage, using ultraviolet radiation to kill mold and other fungi. California Indian people used a hammerstone to crack open acorns placed on a flat rock (Driver 1952). The Karuk kept hulled tanoak acorns in their homes after drying them on basket plates. The drying acorn meats were occasionally shaken and then rubbed and winnowed to remove their thin skins (Schenck and Gifford 1952).

Outdoor storage allowed for significant stockpiles. Many tribes created granaries to store excess acorns for future daily use, feasts, and trading. Sometimes these were long distances from a village. Made from woven tule (*Schoenoplectus acutus* [Muhl. ex Bigelow] A. Löve & D. Löve var. *acutus*), coppice growth of willow (*Salix* spp.), or other woody plants (wattle) and/or conifer boughs, these silos often perched on branch legs to elevate them off the ground. Construction practices varied among tribes and over time. During the winter months, when fresh foods were scarce, stored acorns took on even greater importance in the diet.

Many preparation methods existed. Initially indigenous peoples only processed the nuts either un-hulled or hulled but never crushed. Multiple tribes immersed or buried acorns whole to extract bitter tasting tannic acid including the Yurok, Hupa, Pomo, and Yuki (Gifford 1968). The Karuk prepared un-pulverized tanoak nuts by placing them in a hole and pouring water over them “for several weeks until they became soft and turned black” (Davis 1991). A southwestern Pomo preparation method involved nuts placed in a pool with the hull cracked but left on. After four or five months, the mushy, tannin-free acorns were hulled and cooked whole (Gifford 1967). As in the preparation of cheese, yogurt, and wine, fungi are sometimes factored into acorn preparation. After several weeks in a Pomo home, hulled but still whole nuts molded. After the greenish patina was rubbed off by hand, women ground the nuts and used them to give dishes a sour flavor much like vinegar and salt (Gifford 1967). Sometimes people roasted or boiled whole nuts, too. However, leaching whole nuts in water or mud required a great deal more processing time to remove enough tannic acid.

Thousands of years ago, women developed a much faster way to process acorns. Pulverizing then leaching became the preferred mode of preparation and dominated where acorns served

as a staple food (Driver 1952). This radically quicker leaching process liberated a “vast new food supply of high nutritive value” (Gifford 1968). In California’s North Coast Ranges, anthropologists have uncovered milling implements as old as 5000–7000 yrs (Basgall 1987). From archeological sites in the southern end of the North Coast Ranges, “the slab and hand-stone represented the primary milling technology until about 3000 B.P., after which the mortar and pestle became increasingly more important” (Basgall 1987). A flat milling slab combined with an elongated stone or mano typically served to grind the small, hard seeds of mostly grassland plants (pinole), while the stone mortar and pestle served primarily to pulverize acorn-meats and other oily nuts (Chartkoff and Chartkoff 1984; Basgall 1987). Oak logs with depressions sometimes served as mortars, too (Driver 1952). In Potter Valley and other areas in northwest California, women used oak mortars (S. Smith-Ferri, Grace Hudson Museum, personal communication, 14 September 2011). They used bottomless basket hoppers on their mortars to keep meal in place during the acorn-pounding process.

The practice of pounding acorns and then leaching the meal with water in a sand basin or basket became widespread between 4000 and 2000 B.C. (Fig. 5) (Chartkoff and Chartkoff 1984). Prior to leaching, Karuk women sifted the acorn meal “in a tight, flat basket, the coarse stuff being removed by tapping the basket with a stick” (Schenck and Gifford 1952). Sifting practices varied among different indigenous peoples, but essentially it involved separating out the still coarse material to repulverize it. During the leaching process, the Karuk used increasingly warmer water. When whites introduced metal pots in the mid-19th century, Round Valley Reservation cooks adapted to leaching almost entirely with warm water to hasten leaching time (Essene 1942). Traditional cultural practitioners persisted with the slower method of using cold water (Essene 1942). Heated water extracts the tannic acid faster, but cold water leaves more of the nutritive value including the high-quality fats. Periodic taste-testing during the leaching process serves to indicate when the bitter tannic acids have been adequately removed. Some people like the taste of a little tannic acid, while others like a more leached acorn food because it tastes “sweet” or bland. Most people eat prepared acorns with salmon, venison, or honey. The preferred consistency of tanoak acorn food varies from a watery soup to a thick porridge.

Worldwide, the acorn-food technologies of California are among the most developed. People across the globe used (and continue to use) acorns from various oak species as food, but tannic acid removal practices varied or were lacking entirely. Indigenous people in central Arizona only ate unleached, sweet acorns, thus



FIG. 5. Mrs. Freddie (Hupa) leaching acorn meal in 1902. To her left appears an open-weave acorn-collecting basket. Courtesy of the Phoebe A. Hearst Museum of Anthropology and the Regents of the University of California. Photograph by Pliny E. Goddard (Neg. No. 15-3329).

neglecting acorns with more tannin that yielded a bitter taste. This was true in Mediterranean regions as well, such as Spain. In Mexico, people neglected acorns entirely as food. Most east coast tribes of North America boiled acorns prior to pulverizing to make them palatable, as did people in Japan. On the island of Sardinia in the Mediterranean Sea, human beings boiled and then ground acorns, but they mixed iron-oxide-rich clay with meal to “counteract the tannic acid” in the same way Pomo women do when making acorn bread from black oak acorns (Gifford 1968). In the southeastern United States and Persia, people pounded then leached acorns like California Indians (Driver 1952).

Once leached of the bitter tannins, Native California women cooked tanoak acorn soup or porridge with hot rocks placed in baskets, using two sticks often with loops at the ends. To avoid burning the baskets, women kept the hot rocks moving with wooden paddles. Cooks used extreme caution in selecting rocks that would not explode when they were dunked in water to rinse off ashes before placing them in the cooking basket (S. Smith-Ferri, Grace Hudson Museum, personal communication). Many women inherited their cooking rocks from female relatives. This method of cooking was fast, and the resulting food was served in dedicated basket bowls or cups. Karuk cooks gave the cake that formed on hot cooking rocks to children as a special treat (Baker 1981). The Kashaya Pomo preferred (and

still prefer) tanoak acorns for cereal and soup, while favoring black oak or valley oak (*Quercus lobata* Née) acorns for unleavened acorn bread prepared in an earthen oven (S. Smith-Ferri, Grace Hudson Museum, personal communication, 14 September 2011). Sometimes the Karuk used hot coals to bake patties from tanoak acorn paste (Baker 1981). Along with other abundant native foods such as pinole and salmon, tanoak acorns made possible a settled existence in a relatively small area. A single, well-tended tanoak grove could meet the needs of a tribal village without supplemental irrigation or inordinate amounts of physical labor (Heizer and Elsasser 1980).

TRADITIONAL ECOLOGICAL KNOWLEDGE

To maximize acorn production, indigenous peoples manipulated vegetation on a landscape scale using fire. Burning practices involving frequent, typically low-intensity fires developed in response to climate change. About 6000–5000 yrs ago a warm, dry spell, called the Xerothermic, facilitated the expansion of oak woodland and prairie on the West Coast. Between 4500 yrs ago to the present, the climate changed again to wetter, cooler conditions, and as a result Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and other conifers spread at the expense of oak woodland and prairie (Briles et al. 2005). Fire favored acorn-producing tanoaks and pinole-producing prairies over conifers. Pinole

was made from a variety of grassland seeds such as tarweed (*Madia* spp.) and California oat grass (*Danthonia californica* Bol.). It is difficult to know how significant acorns were relative to pinole in the indigenous diet prior to American settlement. This is due to the rapid changes in grasslands with the advent of livestock grazing and the conversion to non-native orchard grasses, row crops, and towns. What is clear is that Native peoples engaged in a kind of permaculture and agroforestry using native species. By design they created cultural landscapes with fire, where grassland and tanoak groves thrived in a region naturally dominated by coniferous forests. Evidence for intentional burning exists in the ethnographic record, in the ecological response to fire, and in microfossil research (Bicknell, unpublished). The historic record also provides supporting evidence including serial photographs documenting vegetation change over time (Bowcutt 1994–1996; Bowcutt 2011).

The anthropological literature documents indigenous burning as widespread to favor tanoaks and associated prairie on the North Coast of California. The Lassik kept “much of their territory ... completely clear of underbrush” through frequent, low-intensity ground fires, particularly along the Eel and Mad rivers. According to the informant, “much of Trinity County” was “almost open prairie,” but by 1938 it was “choked with thick brush” (Essene 1942). Ethnographer Llewellyn Loud claimed in 1918 that prairies would have produced forests if the Wiyot Indians didn’t annually burn “so as to gather various seeds, especially a species of sunflower.” The location of these food oases was well known by the Wiyot and they “maintained regular trails between them” (Loud 1918). In addition to making human travel easier, burning cleared the ground before acorn harvesting (Schenck and Gifford 1952; Beard 1979). After completing their acorn harvest, the Tolowa burned the inland tanoak groves that they “heavily exploited” before returning each year to their coastal villages (Gould 1976). Ethnographer Gladys Nomland noted that Sinkyone “[m]en fired grassy meadows” to foster food production (Nomland 1935). Even myths point to burning as a common cultural practice. Alfred Kroeber, Nomland’s professor at the University of California at Berkeley, recorded a Sinkyone story that featured buzzard flying “over the dry grass. Wherever he went, he fired the grass, and the flames spread” (Kroeber 1919). The Pomo Indians of Redwood Valley burned annually to maintain widely spaced oaks with a grassy understory. In their “beautiful park landscape,” burning controlled the brush while leaving “the larger trees ... uninjured” (Kniffen 1939). By decreasing fuel loads, regular burning by tribal peoples reduced the risk of catastrophic wildfire

that would destroy mature tanoak trees (Anderson 2005).

Frequent burns minimized loss of tanoak acorns to diseases, insect pests, and unfavorable climatic conditions. A Karuk woman, Mamie Offield, explained to an ethnographer that annual burning protected tanoak from infection and insects (Schenck and Gifford 1952). It reduces insect populations because trees abort acorns infested with weevil and moth larvae during development, thus a ground fire set after initial acorn drop kills the larvae inside and those already in the leaf litter (Warburton and Endert 1966; Vander Wall 2001). Filbert weevils (*Curculio uniformis*), filbertworm moth larvae (*Cydia latiferreana*), and other insects can destroy over half of the acorn crop (Roy 1957b), particularly in the absence of frequent fires. By clearing underbrush, Indian people maintained good airflow around harvested tanoaks, which reduced loss of flowers and developing acorns to cold temperatures. Unfavorable climatic conditions also provoked the southwestern Pomo to pray for acorns “when hail comes from the north” (Gifford 1967). Tanoak acorns ripen in their second autumn, thus increasing their vulnerability to late frost. Current trends in global climate change indicate that “day-to-day weather has grown increasingly erratic and extreme,” which “could have consequences for ecosystem stability and the control of pests and diseases” (quote from Kelly 2011; see also Medvigy and Beaulieu 2012).

Ecological evidence bolsters the argument that Indian people burned to foster wildlife including species they hunted. Repeated fires favor tanoak over non-sprouters like Douglas-fir (Lewis 1993). The coppice growth after burning from tanoak’s basal burl provided basket materials and browse for deer and elk. Deer and bear fatten on tanoak acorns before winter. Many other wildlife species cache acorns for later consumption, such as squirrels, woodpeckers, and jays. Some animals, such as various salamanders and rodents, use tanoak for cover and/or nesting, while certain mammals prey on tanoak herbivores (Raphael 1987). To leave enough for animals, “many native people in northwestern California ... stop acorn harvest after November” (Hosten et al. 2006). For a partial list of animals that eat tanoak acorns, see Table 2.

Research based on microfossils provides evidence that vegetation has shifted in relation to changing climate and fire frequency over the last 15,000 yrs. Pollen cores extracted from wetlands in the Siskiyou Mountains of Oregon indicate that during the last glacial period (>10,900 cal yr B.P.), subalpine forest extended to lower elevations and latitudes than it does today. During the early Holocene (ca. 10,900–4500 cal yr B.P.), the climate shifted to “warmer-and-drier-than-present summer conditions,” favoring xerophytic

TABLE 2. SOME WILDLIFE SPECIES THAT CONSUME TANOAK ACORNS (ROY 1957A; FRYER 2008; ITIS 2011).

Animal type	Common name	Scientific name
Birds	acorn woodpecker	<i>Melanerpes formicivorus</i>
	band-tailed pigeon	<i>Patagioena fasciata fasciata</i>
	varied thrush	<i>Ixoreus naevius naevius</i>
	Steller's jay	<i>Cyanocitta stelleri</i>
Mammals	American black bear	<i>Ursus americanus</i>
	California ground squirrel	<i>Spermophilus beecheyi</i>
	Columbian black-tailed deer	<i>Odocoileus hemionus columbianus</i>
	Douglas squirrel	<i>Tamiasciurus douglasii mollipilosus</i>
	dusky-footed woodrat	<i>Neotoma fuscipes fuscipes</i>
	mule deer	<i>Odocoileus hemionus</i>
	northern flying squirrel	<i>Glaucomys sabrinus</i>
	raccoon	<i>Procyon lotor</i>
	Townsend's chipmunk	<i>Tamias townsendii</i>
	western gray squirrel	<i>Sciurus griseus</i>

species such as oaks and chinquapin (Briles et al. 2005). Xerophytic vegetation contracted when the climate became cooler and wetter during the late Holocene (ca. 4500 cal yr B.P.–present), except where burned regularly by Native peoples. Fossilized pollen of tanoak resembles chinquapin pollen, making fine-grained vegetation reconstruction difficult (Briles et al. 2005). However, pollen evidence indicates that indigenous burning changed vegetation elsewhere in the West. For example, in Yosemite Valley, *Quercus* pollen begins to increase about 700 yrs B.P. despite climatic conditions that favored fir (*Abies*). Archeological evidence indicates indigenous peoples of Yosemite Valley became more dependent on oak acorns between 650–750 B.P., thus giving them an incentive to burn frequently to kill pines. “At contact [with Euro-Americans], much of the valley was an open oak-grassland with few conifers. However, after nearly three-quarters of a century of fire suppression or exclusion, the valley was choked with shrubs and young conifers” (Anderson and Carpenter 1991).

Paleobotanical research based on phytoliths, another kind of microfossil, indicates that coniferous forests and coastal scrub have expanded with fire suppression over the last century on the northern coast of California. Humboldt State University professor Susan Bicknell found an abundance of phytoliths unique to grasses in areas now dominated by conifers in Sinkyone Wilderness State Park on the northwestern Mendocino coast (Bicknell unpublished). These silicon dioxide deposits originate between and inside plant cells and can persist in the soil for millions of years. Researchers use phytoliths to study vegetation change over time. Bicknell and her graduate students also found Douglas-fir seedlings, saplings, and trees in nearly all their grassland and scrub plots, which lead them to conclude that this conifer could naturally occupy most sites in the park.

The historic record documents prohibitions on indigenous burning and the radical transforma-

tion in vegetation that followed. In regions of California colonized by Spaniards, the “civil authorities issued edicts, such as Governor Arrillaga’s command in 1793” that prohibited burning “to increase the productivity of wild foods” (Lightfoot 2005). In Humboldt Co., a geographic area in northern California with an abundance of tanoaks, the Euro-American settlers of the Mattole Valley passed a resolution in 1858 that the Indians “not set fire to the grass” (Bledsoe 1885). A collector of wild lily bulbs for the horticulture trade watched as beds he sustainably harvested over multiple years ultimately became overgrown and shaded out during the 1870s due to suppression of indigenous burning (Anderson 2005). Prohibition of Indian-set fires to manage the underbrush in Mendocino Co. caused a shortage of suitable basket-making materials, which was noted by a basket dealer in 1923 (Anderson 2005). Photographs taken over the last century document an increase in Douglas-fir and coastal scrub in Sinkyone Wilderness State Park at the expense of coastal prairie and associated tanoaks (Bowcutt 1994–1996).

Willis Linn Jepson, a University of California botany professor from 1899–1937, noted in 1910 that coniferous forests dominated more acreage in the West than when whites first arrived (Jepson 1910). Even prior to the ability to suppress fires on a landscape scale, the consequences of fewer human-set fires became apparent within decades of American settlement. Compared to resinous conifers, tanoaks are less flammable. Jepson claimed that, “fires rarely kill tanbark oak trees” (Jepson 1911). He wrote that trees more than 100 yrs old develop “long vertical wounds,” which generally spread. However, if it does die down to the ground, tanoak resprouts from burls at the base of the trunk. Although seedlings are fire sensitive, scars heal over on surviving young trees (Jepson 1911). Mature, ridgeline tanoaks enjoy the most benefits from frequent burning. According to Jepson, “about 80 percent are comparatively free from fire hollows, because a



FIG. 6. Essie Parrish gathering acorns. Kashaya, Sonoma Co., California, 1960. Courtesy of the Phoebe A. Hearst Museum of Anthropology and the Regents of the University of California. Photograph by Josepha Haveman (Neg. No. 15-19440).

fire traveling up a slope is either running high or going out when it reaches the top" (Jepson 1911). Speaking in general about California forests, he noted that annual burning favors "under certain conditions the development of large individual trees." In contrast, even five to ten years of fire suppression resulted in fuel accumulation that could lead to destructive fires that "injure more severely or even consume large trees." Jepson concluded that, based on their skillful use of fire as a management tool, "some credit must be given to the native tribes as foresters" (Jepson 1909).

CONTEMPORARY INDIGENOUS USE OF TANOAK ACORNS

Native people have continued to use tanoak acorns for human food since American colonization, albeit at a reduced scale. Assimilation efforts beginning in the late 1800s resulted in most Native people shifting to wheat as a staple. However, the early reservations were notorious for being unable to reliably feed, shelter, and clothe Indians. Reliance on wild foods continued and persists today. In 1938 a Lassik informant told a University of California

anthropologist that "[i]f the Indians ain't got acorns, it seem like he ain't got nothing" (Essene 1942). Lulu Johnson, a Yuki woman, still prepared tanoak—or *shō'-kish*—acorn soup, mush, and pancakes for her family in the 1950s when they had "a longing for the taste of the nuts" (Curtin 1957).

In 1964, anthropologist Samuel Alfred Barrett produced a film on tanoak acorn use as part of the American Indian Film Project. Entitled *The Beautiful Tree, Chishkale*, it was made in collaboration with a Kashaya Pomo leader, Essie Parrish, and her family (Barrett 1964) (Figs. 6, 7). Barrett focused on what he perceived as authentic practices and intentionally did not document the adaptation of new tools like shovels, rakes, metal meat grinders, and pots to facilitate acorn harvesting and processing (S. Smith-Ferri, Grace Hudson Museum, personal communication). In reality, beginning in the mid-19th century, indigenous women had creatively repurposed the garden and culinary tools of Euro-American culture to serve their needs when obtaining and preparing tanoak-based foods.

While fire suppression, livestock grazing, and development diminished acorn crops throughout



FIG. 7. Essie Parrish preparing acorn meal. Kashaya, Sonoma Co., California, 1960. Courtesy of the Phoebe A. Hearst Museum of Anthropology and the Regents of the University of California. Photograph by Josepha Haveman, (Neg. No. 15-19554).

California, increasingly during the 20th century, the automobile facilitated travel to locations where the greatest number of acorns could be gathered which might vary from year to year. Some people shifted their collecting to mowed landscapes such as cemeteries to facilitate the process. Others were forced to gather at higher elevations than their ancestors had gathered, which often shifted the required schedule to ensure ripeness. Adaptability continues to be key to the efforts of keeping tanoak food traditions alive and vibrant.

Dishes made with tanoak acorns are still served at celebrations, tribal gatherings, and as a healing food for the sick and elderly (Fig. 8) (McCarthy 1993). Many health practitioners argue that adoption of a Western-style diet has contributed to the high rates of diabetes among indigenous people. According to the Centers for Disease Control and Prevention, "American Indian and Alaska Native adults are 2.6 times more likely to have diabetes than non-Hispanic whites of similar age" (CDC 2011). Medical research links diabetes with diets high in simple carbohydrates and low in healthy fats. Speaking in 1984, Hoopa tribal

woman Winnie Marshall warned that in the future "everyone might have to rely on native foods to survive" (Marshall 1984). Note that Hoopa Valley tribal members may or may not be of Hupa ancestry. Unfortunately, most legacy tanoak trees were destroyed by the tanbark industry supplying tanneries between the 1840s and 1920s. And in the 1950s, softwood producers began poisoning tanoak with herbicide to favor marketable conifers in industrial forests (Bowcutt 2011).

Reviving old acorn economies is part of a worldwide movement of indigenous peoples uniting around issues of "cultural survival, ownership of knowledge or intellectual property rights, empowerment, local control of land and resources, cultural revitalization, and self-determination" (Berkes 1999). Many tribal peoples lost access to tanoak acorns through government land appropriation and relocation policies in the 19th century that moved tribes to inland locations that lacked dense, productive populations of the tree. Many California tribal people feel plants thrive in positive relationships with people (Anderson 1993). Tribal elders contend that "plants want to be used," and if



FIG. 8. Cooking tanoak acorns in fall 2011, from left to right Kayla Carpenter, Gina Balabas, and Melodie George-Moore, all Hupa Tribal members. Photograph by Laura Lee George.

they aren't, their quality deteriorates and their numbers diminish (Anderson 1993). For tanoak to thrive, human intervention with good intentions and skillful means may be required.

Native peoples rely on this important food source and are proactively seeking ways to foster tanoak well-being. Unfortunately, the possibilities for reestablishing managed tanoak acorn trees are limited. The densest stands occur in northwestern California near the coast, most of which are not on existing reservations or rancherias. A Pomo Indian said in a 1995 interview that his grandparents traveled some distance from Sherwood Rancheria to harvest roughly 135–180 kg of tanoak acorns from the same tree each year (Bowcutt 1996). The Karuk, Yurok, and Hoopa Valley Tribes have reintroduced burning on their tribal land to foster tanoak acorn production. The Hoopa also manually thin on their land to favor broad tanoak canopies for increased acorn production (Wilkinson et al. 1997). To create a productive, wide tanoak crown, foresters recommend thinning lightly over a period of time to avoid damaging trees by sudden exposure to sunlight after logging (McDonald and Tappeiner 1987; McDonald and Huber 1995).

The InterTribal Sinkyone Wilderness Council (hereafter, Council) was formed in 1986 to

protect and preserve Sinkyone ancestral lands, and to revitalize local tribes' cultural land-stewardship practices (Bowcutt 2011). The ten federally recognized tribes in the Council include the Cahto Tribe of Laytonville Rancheria, the Coyote Valley Band of Pomo Indians, the Hopland Band of Pomo Indians, the Pinoleville Pomo Nation, the Potter Valley Tribe, the Redwood Valley Rancheria of Pomo Indians, the Robinson Rancheria of Pomo Indians, the Round Valley Indian Tribes, the Scotts Valley Band of Pomo Indians, and the Sherwood Valley Rancheria of Pomo Indians. In 1997, the Council purchased from The Trust for Public Land approximately 1556 hectares of aboriginal Sinkyone Indian land adjacent to the coastal Sinkyone Wilderness State Park. The Council's goals include reestablishing traditional stewardship of native species, such as tanoak, and reintroducing culturally informed prescriptive burning of coastal prairie and tanoak groves to improve tanoak health. This approach is consistent with contemporary ecological restoration of *Quercus*-dominated woodland, which often combines manual removal and prescribed fire "to reduce conifer density" (Fig. 9) (Reid and Sugihara 1987; Hosten et al. 2006).

SUDDEN OAK DEATH THREAT

Diseased and dying tanoak trees were first noticed in the mid-1990s north of San Francisco in Marin Co. around Mount Tamalpais (McPherson et al. 2005). Plant pathologists ultimately concluded that a previously undescribed species was causing the observed bleeding stem cankers. The new lethal tanoak pathogen, *Phytophthora ramorum*, is not native to North America, but no one knows where it originated or when it arrived (Grünwald et al. 2012). *Phytophthora* means "plant destroyer," an apt name given the tanoak die-offs it has caused. By 2001, SOD had "reached epidemic proportions in forests along approximately 300 km of the central coast of California," from the Big Sur Coast to Sonoma Co. (Rizzo et al. 2002b). The water mold has spread through commerce in horticultural plants (Rizzo et al. 2005; Ivors et al. 2006; Marscheretti et al. 2008). Although tanoak has proved to be the most susceptible, many native California species and common nursery and landscape plants serve as carriers that help spread the pathogen (Rizzo et al. 2002a). Of the ornamental hosts most prone to spread the disease, plant pathologists list three genera in the Ericaceae (*Rhododendron*, *Pieris*, and *Kalmia*), *Camellia* (Theaceae), and *Viburnum* (Caprifoliaceae) (Frankel 2008). While fatal to tanoak and some other related tree species, most of its hosts suffer only shoot die-back or leaf spots and blotches. (An updated list of host plants is available at www.suddenoakdeath.org).



FIG. 9. Underburning in a tanoak stand in Humboldt Co., California, near the town of Orleans. Orleans/Somes Bar Fire Safe Council [OSB-FSC] implemented a prescribed burn in October 2010. Workers tending to the fire are Ben Beaver and Will Harling. Photograph by Frank Lake.

Researchers believe *P. ramorum* was introduced on imported nursery stock for North American gardens. Increased global trade is accelerating the worldwide spread of exotic diseases, which damages biodiversity and habitat health (Vitousek et al. 1996; Brasier 2008). According to Clive Brasier (2008), a senior plant pathologist,

major problems may arise if a pathogen escapes – or is introduced – to another region of the world where the native plants have little resistance and the pathogen has eluded its natural enemies. Such events can trigger damaging disease episodes that may also have long-term negative impacts on the environment, economy and cultural heritage. Movement of plants and plant products between biogeographical zones by human activities is now generally accepted to be the primary mode of introduction of exotic pathogens and pests. There is therefore a tension, in terms of risk to the cultural and natural environment, between the conservation and environmental responsibilities of horticulturalists, foresters, garden designers and landscape architects and their

desire for novel material or (these days) cheaper plants and instant trees.

Ecosystem change can occur relatively rapidly through novel pathogens. “Starting around 1910 an introduction of *Cryphonectria parasitica*, the cause of chestnut blight indigenous to China and Japan, resulted in the virtual destruction of American chestnut forests (*Castanea dentata*) through most of their natural range in the USA within thirty years” (Brasier 2008). Protections against future importations have been weakened just as the rate of global trade in potted plants and other risky materials has increased significantly. During the Clinton Administration, the federal government repealed the Plant Quarantine Act of 1912, originally passed to prevent another massive, native-tree die-off caused by an introduced pathogen. According to agricultural economist Edward A. Evans, the Plant Protection Act of 2000 superseded it to mirror more closely “the general provisions of the World Trade Organization’s Sanitary and Phytosanitary Agreement” to foster international trade (Evans 2004).

Currently in North America, *P. ramorum* is only reproducing asexually, which limits the

organism's capacity to adapt to changing environmental conditions. However, this could change. Two mating types and several lineages exist in North America with the NA1 (A2-mating type) predominating. The more virulent EU1 (A1-mating type), a strain from Europe, is found in a few "nurseries in California, northern Oregon, Washington, and British Columbia, Canada" (Kliejunas 2010). It has also escaped to a waterway in Humboldt Co. (Frankel 2008). The EU1 (A-1 mating type) has been found in forests in the United Kingdom and is common in European nurseries. Repeated introductions of contaminated European nursery plants have occurred despite monitoring of international trade (Goss et al. 2011). Based on efforts to mate EU1 (A-1 mating type) and NA1 (A-2 mating type) in the laboratory, it is unclear whether *P. ramorum* has a functional sexual breeding system (Brasier and Kirk 2004). If it does, the potential remains for greater disease vigor "if genetic exchange occurs between the European and American subpopulations" (Brasier and Kirk 2004). Despite the high rates of abortion, viable oospores appear to form, which means that "coexistence of both mating types on adjacent plants increases the chances for sexual recombination between these two genetically divergent lineages" (Garbelotto et al. 2006). Another indication that the impact of SOD on tanoak could worsen is that, currently, the less aggressive lineage is the more prevalent one in North America. Although rare, two other, "generally more virulent" lineages already occur in North America (Kliejunas 2010).

Based on multiple computer models, the coastal counties of Mendocino, Humboldt, and Del Norte are at high risk for widespread *P. ramorum* infection. Mild temperatures and high rainfall favor the pathogen. Also, multiple host plants grow in the region, including salal (*Gaultheria shallon* Pursh) and huckleberries (*Vaccinium* spp.). Although *P. ramorum* sporulates on a wide variety of host species, some species play more important roles in spreading the disease. California bay (*Umbellularia californica* [Hook. & Arn.] Nutt.) significantly increases disease risk, leading some researchers to advocate for its removal to reduce risk to neighboring oaks (Kliejunas 2010). Although its production of asexual spores isn't typically as prolific as California bay, tanoak too can inoculate forests with *P. ramorum*, particularly through sporangia production on leaves and twigs. Spore production begins with winter rains or shortly thereafter. Sporulation peaks with warm, spring rains and drops off to zero with hot, dry summer weather. However, in coastal areas with summer fog, inoculum persists year round (Kliejunas 2010). Wind-blown rain can assist the spread of spores. Loss of productive tanoak trees to SOD is

already negatively impacting tribal communities in Sonoma Co., having spread to Kashaya Pomo Indian lands probably from neighbors who planted infected rhododendrons (D. Rizzo, University of California, personal communication). Thousands of trees have died near their 40-acre Stewarts Point Rancheria where families still harvest tanoak acorns (Ortiz 2008).

Through regulation of interstate nursery trade, the U.S. Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) strives to prevent SOD spread "to noninfested areas of the United States" (Knighten and Redding 2004). In 2005, APHIS began requiring that California, Oregon, and Washington nurseries shipping "host plant nursery stock interstate, be inspected and certified free of evidence of *P. ramorum*," after four West Coast nurseries "shipped potentially infected stock to over 1200 nurseries in 39 states" (Kliejunas 2010). In regulated areas, growers must destroy infected plant material (APHIS 2010). In 2001, only one California nursery tested positive for *P. ramorum*, but by 2004 that number jumped to 176 in multiple states (Frankel and Hansen 2011). The number dropped to 34 by 2010 after APHIS began regulating the three states with known infected nurseries. But based on field investigations in 2009, *P. ramorum* spread to streams outside infested nurseries in five states (Washington, Mississippi, Alabama, Georgia, and Florida) (Frankel and Hansen 2011). A number of southeast U.S. forest species are vulnerable to *P. ramorum*, including 18 species of red oak (*Quercus* spp.), which became dominant after the demise of American elm (*Ulmus americana* L.) and American chestnut (Kluza et al. 2007). *Phytophthora* spp. that can infect forest plants are a biosecurity threat. As a result, APHIS established a protocol in 2006 for responding to *P. ramorum* outbreaks in forest and wildland environments; however, as of 2011, "no Federal response protocol for new wildland incursions" exists (Frankel and Hansen 2011). "The continued spread of this and other new *Phytophthora* spp. presents significant impetus for adjustments in the management and regulation of forest pathogens and nursery stock" (Frankel 2008).

Despite the federal quarantine administered by APHIS, various states have attempted to establish supplemental quarantines to protect their natural resources and industries. However, APHIS has yet to approve a "special need request" or SNR. A review of APHIS administration of the SOD quarantine indicates that "the SNR process has not achieved Congress' goal of allowing limited state regulation that is more restrictive than federal requirements" (Porter and Robertson 2011). Read Porter, a senior attorney with the Environmental Law Institute and Nina Robertson, a law clerk with the U.S. District

Court for the District of Columbia, defend states' rights in protecting against invasive species and call for an improved SNR process to avoid "the spread of pests into areas where they are not yet present but are likely to cause substantial harm to the economy and environment." Currently, the interests of industry prevail according to Porter and Robertson (2011). "By focusing on facilitation of trade and reduction of risks rather than prevention, Congress in effect created a preference for leaky quarantines and for trade over environmental protection." Nor have the courts upheld states' rights to reduce the risk of *P. ramorum* infection. In 2004, the California Association of Nurseries and Garden Centers sued and won to block Kentucky and nine other states from enforcing their own SOD quarantines on horticultural products shipped from California, interstate commerce valued at roughly \$500 million annually (Hirsch 2004). Justice James McReynolds may prove prophetic when he warned in 1926, "[i]t is a serious thing to paralyze the efforts of a state to protect her people against impending calamity, and leave them to the slow charity of a far-off and perhaps supine federal bureau" (Oregon-Washington Railroad & Navigation Company v. Washington, 270 U.S. 87, 103 [1926], Justices McReynolds & Sutherland dissenting, as cited in Porter and Robertson 2011).

Quarantines and vigilance provide some protection for our forests from exotic disease species. But their effectiveness is limited for a number of reasons. Current methods of testing are not sensitive enough to reliably and consistently detect them (Brasier 2008). Furthermore, predicting destructive foreign organisms is not always possible because "most are unknown or innocuous in their native forests" (Schowalter et al. 1997). Confirmation of *P. ramorum* requires culturing and microscopy or molecular analysis, which can delay detection. Unfortunately, some nurseries are noncompliant with regulations and/or best practices (Brasier 2008), plus only a tiny fraction of the landscape plants produced for sale are tested. Because the detection of potential plant pathogens is difficult, Evans (2004) calls "the potential gains from [international] trade ... questionable." Susan Frankel, the SOD Research Program leader for the U.S. Forest Service, and Everett Hansen, an Oregon State University SOD researcher, note that "tools designed to protect forests and nurseries need refinement" (Frankel and Hansen 2011). Brasier (2008) more urgently calls for reform because global market influences have contributed to making "international plant biosecurity protocols ... outmoded, flawed, institutionalized, and too ineffectual." He advocates that they "be fully scientifically reviewed and appropriately overhauled, taking full account of the underlying scientific weaknesses and of the many other causes of security failure" (Brasier 2008).

SUDDEN OAK DEATH RESPONSE

Given our inability to prevent all introductions of exotic diseases, plant pathologists advocate quick response to early detections to limit their impact (Meentemeyer et al. 2004; MacLeod et al. 2010). In an effort to reduce *P. ramorum* spore production and subsequent spread, the Oregon Department of Agriculture required removal and burning of "all infected plants and all host plants growing within a 15–30 m buffer zone beyond symptomatic tanoak trees" near the town of Brookings (Curry Co.). The treatment typically includes herbicides to limit tanoak resprouting (Hansen et al. 2008). Oregon's infestation, as well as disjunct outbreaks in Mendocino and Humboldt counties in northern California, concern scientists given their potential to catalyze landscape-scale infection in a high-risk area. An infection near the town of Redway (Humboldt Co.) is worrisome to plant pathologists since it is a significant distance from other infestations and provides a northern foothold for the pathogen in California (Fig. 10) (Meentemeyer et al. 2011). Of even greater concern is an infection found farther north outside of Redwood National Park (NPS 2013). "In the absence of extensive control," Meentemeyer et al. (2011) "predict a ten-fold increase in disease spread between 2010 and 2030 with most infection concentrated along the north coast between San Francisco and Oregon". As a result, "substantial tree mortality, particularly of tanoak, is likely to follow." Based on their computer model, they predict "explosive growth in infection and disease ... to occur around 2016." Although it is unlikely that *P. ramorum* will cause tanoak extinction, it will likely cause "the rapid and extensive loss of overstorey trees ... within 30 years of pathogen establishment in many forests" (Cobb et al. 2012).

Pesticides cannot feasibly be used to control SOD on a landscape scale. Many pesticides used on other species in the genus *Phytophthora* test as effective against *P. ramorum* under experimental conditions (Kliejunas 2010). Currently Agri-Fos® is recommended as a prophylactic if applied twice in the first year and then annually after that (Kliejunas 2010). In rugged areas with limited access, intensive pesticide treatments are prohibitively expensive if commercial applicators are used or if the work is logistically difficult. Plus, pesticide use is widely unpopular in northern California and poses a significant political liability for those proposing synthetic chemical intervention (Van Strum 1983; Bowcutt 1999). Future use of pesticides in forest settings requires public support (Whitfield 1992).

FIRE AND FOREST PATHOGENS

The health status of a particular tree may not be a significant factor in the SOD epidemic

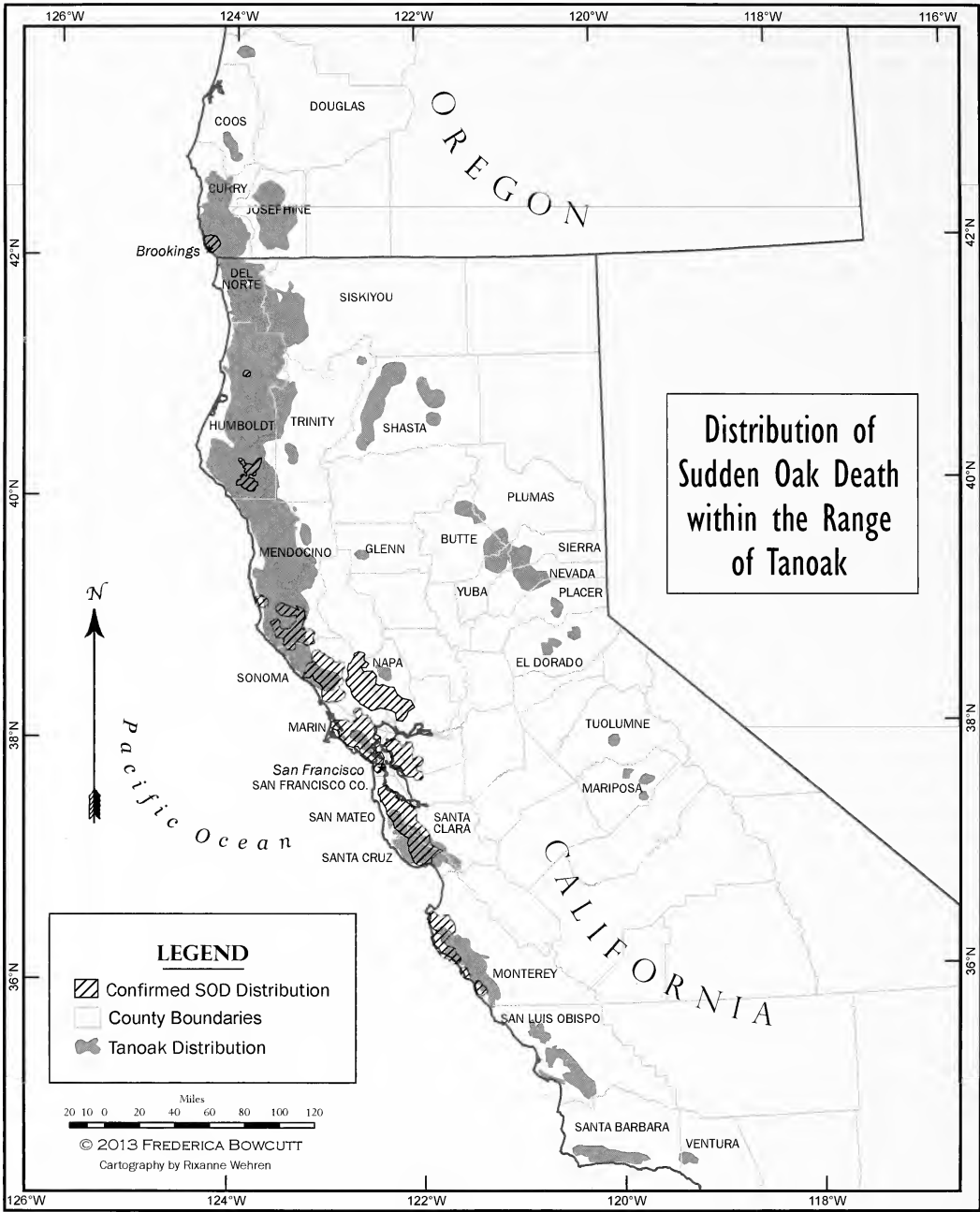


FIG. 10. Sudden oak death distribution in relationship with tanoak distribution. Data sources: data on California and Oregon distribution as of February 20, 2012 came from Geospatial Innovation Facility (2012). A few additional sites were added from U.C. Berkeley Forest Pathology and Mycology Laboratory (2012). Oregon sudden oak death distribution as of March 14, 2012 came from the Oregon Department of Agriculture (2012). The tanoak distribution data for California came from Griffin and Critchfield 1976. Tanoak distribution data for Oregon came from the Oregon Flora Project (2012).

because *P. ramorum* is a novel pathogen in North America, and tanoak currently exhibits little resistance. However, other forest insect and disease epidemics often link to “environmental stresses that predispose trees to being attacked and killed by secondary agents” (California Oak Mortality Task Force 2011). In Yosemite Na-

tional Park, termination of natural and Native American fire regimes caused colonization of oak woodlands by conifers, resulting in increased competition for light, water, and nutrients. “As oaks have become stressed due to suppression by encroaching conifers, they have succumbed to several canker rots” (Rizzo and Slaughter 2001).

Prior to Euro-American settlement, Native peoples burned Yosemite Valley to control for black oak diseases and to release oaks from conifer competition. A 2005 study suggested tanoak vulnerability to SOD increased with fire exclusion (Moritz and Odion 2005). However, these results have been challenged given the limitations of SOD distribution and fire-history maps, which make studying the relationship between “pathogen invasion and persistence” and burning difficult (Lee 2009).

Fires don’t appear to immunize forests. Nor do prescribed burning or catastrophic wildfires eliminate *P. ramorum* from a site, though they can reduce its spread (Lee 2009). Preliminary results from experimental treatments in southwestern Oregon and northern California forests suggest “that burning can be a valuable tool in cleaning up small infectious material in infested sites,” even when it doesn’t eliminate the pest (Lee 2009). Thus far, frequent, low-intensity fires that mimic traditional ecological practices of indigenous peoples experienced with managing tanoak have not yet been tested as a prophylactic measure or to treat an infected site. Many California Indians are deeply committed to continued use of tanoak acorns and seek partnerships to address the *P. ramorum* threat (Ortiz 2008). An increasing number of commentators question exclusively relying on scientific expertise at the expense of other forms of knowledge when making decisions about environmental issues that impact stakeholders. They advocate for “partnerships between experts, policy advisers and stakeholders” that embrace “participatory approaches” (MacLeod et al. 2010).

TANOAK CULTURAL LANDSCAPES

Existing public lands provide opportunities for safeguarding tanoak. However, many are already infested with the SOD pathogen (Appendix 1). Park visitors and neighboring gardeners unwittingly have become disease vectors. Establishing management practices designed to reduce infection risk in uninfected parks on the north coast of California makes sense given that scientists predict explosive disease expansion in this region. Redwood National and State Parks (RNSP) are at high infection risk due to multiple vehicular entry points and high visitation combined with a favorable climate and an abundance of suitable hosts. Redwood Creek has tested positive for *P. ramorum* in the park. Although no plants appear diseased, the “infection source is approximately 5 mi (8 km) southeast of the Park boundary and could eventually move into RNSP forests” (NPS 2013). RNSP natural-resource managers are preparing for “the inevitable arrival of *P. ramorum* to the parks” by adopting preventive measures to slow its spread once it arrives. Park managers recognize tanoak as a valuable ecolog-

ical component of the coast redwood forest in the park. “RNSP also has an important cultural legacy of large stands of old tanoak trees that have been managed by Native American families for many generations” (Bueno et al. 2010). Park managers are considering “creating tanoak refuges (defined as tanoak groves that are least likely to become infected due to spatial or temporal factors)” (Bueno et al. 2010). Based on epidemiological modeling, widely spaced tanoaks associated with plants that are immune to *P. ramorum* infection “resulted in slow-enough transmission to retain overstorey tanoak” (Cobb et al. 2012). Manipulating vegetation to create conditions unfavorable to the pathogen prior to disease arrival could radically reduce risk.

Sinkyone Wilderness State Park could serve as another tanoak refuge in this North Coast zone of high risk. It occurs on the longest stretch of undeveloped coastline in the 48 contiguous states with a large buffer of undeveloped land. Limited road access makes temporary park closures feasible during the period the disease is most active (March–May) to reduce the risk of humans accidentally spreading the disease. The watersheds in the park are minimally developed further reducing the risk of infected waterways spreading the pathogen. Introduction of infected nursery plants in the area is less likely due to the low number of neighboring ranchettes. Although the park appears to be uninfected, new outbreaks are increasingly encroaching (Peterson 2012), so reducing infection risks now may safeguard tanoaks. A risk-reduction plan could be developed based on current best practices, including prohibiting potentially contaminated material in tanoak cultural landscapes. Given that the ethnographic record indicates annual, low-intensity ground fires can be effective against other kinds of tanoak diseases, it is worth investigating if this traditional ecological knowledge could help address the current SOD crisis.

Case studies from western North America offer us models of how partnerships involving tribal groups can help to repair environmental and social damage. For example, the Nisqually Tribe, the U.S. Fish and Wildlife Service, and several non-profit organizations restored the Nisqually River Delta to an estuary 100 years after it was diked for agriculture (Middleton 2011). Within the Six Rivers National Forest, Yurok, Karok, and Hoopa elders advised on “a series of experimental burns to enhance the quality and quantity of ... beargrass,” which is used by tribal members for basket making (Anderson 1993). These partnerships didn’t restore what’s been lost, but they did begin to heal the damage. Given significant changes to forest systems, reintroducing fire alone won’t address the challenges facing tanoak. Any potential benefits will need to be weighed against the risks, but that

analysis needs to occur in a way that involves Native people with a stake in tanoak wellness.

CONCLUSIONS

Concerted action is needed due to the threat posed by *P. ramorum*. Tanoak plays key roles in coast redwood forests and other ecosystems. It is the most abundant hardwood in California, the only species in its genus, and its acorns still serve Native peoples as a beloved, indigenous food. Fortunately, the heartland of tanoak's distribution is mostly uninfected. Timely intervention is important because of tanoak's ecological and cultural significance. To be fully successful, actions to protect tanoak should:

- involve tribal leadership in each step of its development and implementation,
- make recommendations on infection risk reduction strategies for tanoak cultural landscapes,
- address widespread concerns about pesticide use,
- suggest policy changes to address the continued spread of *P. ramorum*, such as greater restrictions on the movement of susceptible garden plants, and
- develop plans for testing traditional ecological knowledge—namely frequent, low-intensity fires—for treating infested sites and reducing infection risk.

We need to proactively safeguard and cultivate local food sovereignty, including the use of perennial native plants. Used in this way, tanoak might more accurately be called by its other common name: sovereign oak.

ACKNOWLEDGMENTS

The Evergreen State College awarded the author a grant to fund this research during summer 2011. I am grateful to the following individuals who read drafts of this article and gave valuable feedback: Tamara Caulkins, Lisa Hintz, Judith Larner Lowry, Rob Saecker, and three anonymous reviewers. Hawk Rosales, executive director of the InterTribal Sinkyone Wilderness Council, and Dr. Sherrie Smith-Ferri, executive director of the Grace Hudson Museum, commented on sections pertaining to Native peoples. Dr. Dave Rizzo, University of California plant pathologist commented on an earlier version of the section discussing SOD. I am particularly thankful for the insightful feedback and gracious support I have received from Susan Frankel, SOD Research Program leader, USDA Forest Service, Pacific Southwest Research Station.

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APPENDIX I

PARTIAL LIST OF SUDDEN OAK DEATH INFECTED PUBLIC LANDS IN THE RANGE OF TANOAK

Based primarily on data from Dr. Maggi Kelly and Sam Blanchard, University of California, Berkeley, Department of Environmental Science, Policy, and Management. The Siskiyou National Forest, Oregon, infestation is according to the California Oak Mortality Task Force (2012). Abbreviations: BLM = Bureau of Land Management, MA = Management Area, NF = National Forest, NM = National Monument, NP = National Park, NRA = National Recreation Area, NS = National Seashore, OSD = Open Space District, OSP = Open Space Preserve, RA = Resource Area, RP = Regional Preserve, SF = State Forest, SHP = State Historic Park, SP = State Park, SNR = State Natural Reserve, SR = State Recreation Area, W = Wilderness. *The list of county and regional public lands is significantly abbreviated. Infected city lands are not listed.

Federal Lands: Coos Bay District, Myrtlewood RA (Oregon BLM), Golden Gate NRA, Lacks Creek MA (California BLM), Los Padres NF, Ventana W, Muir Woods NM, Presidio of San Francisco NP, Point Reyes NS, Rogue River-Siskiyou NF.

State Lands: Andrew Molera SP, Angel Island SP, Annadel SP, Armstrong Redwoods SNR, Austin Creek SRA, Big Basin Redwoods SP, Bothe-Napa Valley SP, Cape Sebastian SP, Castle Rock SP, China Camp SP, Fort Ross SHP, Hendy Woods SP, Henry Cowell Redwoods SP, Humboldt Redwoods SP, Jack London SHP, John B. Dewitt Redwoods SR, Julia Pfeiffer Burns SP, MacKerricher SP, Mailliard Redwoods SR, Mount Tamalpais SP, Navarro River Redwoods SP, Olompali SHP, Pfeiffer-Big Sur SP, Salt Point SP, Samuel P. Taylor SP, Soquel Demonstration SF, Sugarloaf Ridge SP, The Forest of Nisene Marks SP, Tamales Bay SP.

County and Regional Lands*: Anthony Chabot Regional Park, Bear Creek Redwoods OSP, Briones Regional Park, Coal Creek OSP, Crystal Springs Watershed, El Sereno OSP, Huckleberry Botanic RP, Ignatio Valley OSP, Jacobs Ranch OSP, Jasper Ridge Biological Preserve, Las Trampas Regional W, Long Ridge OSP, Los Trancos OSP, Manzanita Regional Park, Marin Municipal Water District lands, Midpeninsula Regional OSD, Mill Creek Redwood Preserve, Monte Bello OSP, Mount Burdell OSP, Palo Corona Ranch Regional Park, Rancho San Antonio OSP, Redwood Regional Park, Roys Redwoods OSP, Russian Ridge OSP, Sierra Azul OSP, Sobrante Ridge RP, Tilden Regional Park, White Hill OSP, Wildcat Canyon Regional Park.

COULD TANOAK MORTALITY AFFECT INSECT BIODIVERSITY? EVIDENCE FOR INSECT POLLINATION IN TANOAKS

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ABSTRACT

Tanoaks, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh, are being killed by sudden oak death, caused by the pathogen *Phytophthora ramorum* Werres, de Cock & Man in't Veld. However, very little is known about the basic ecology of the species. Here we investigate the pollination ecology of tanoaks using insect-visitor observations along with a pollinator-exclusion study. Insect-visitor observations were conducted by citizen-scientist volunteers at three different sites in the Midpeninsula Regional Open Space District lands in the Coast Range of California in 2009. Pollinator exclusions were conducted over two years (2009, 2010), using veil bags to prevent insects from reaching female flowers at the Blodgett Forest Research Station in the Sierra Nevada foothills. Microsatellite markers were used to infer selfing or outcrossing for the developing acorns. The citizen scientists observed 148 insect visitors to tanoak flowers over 11.5 hours of observation (in 65 observation periods). Pollinator exclusion resulted in lower fruit set and higher rates of selfing. The data suggest that tanoak is primarily an insect-pollinated species, though some level of wind pollination is likely. There is a diverse community of insects visiting tanoak flowers. In order to understand the importance of tanoaks to the native insect community, future research needs to focus on identifying the composition of the insect community, and the extent to which they rely on tanoak pollen and nectar as a food source.

Key Words: Flowering phenology, insect observations, insect pollination, *Lithocarpus densiflorus*, *Notholithocarpus densiflorus*, pollinator exclusion, tanoak.

Tanoaks, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), across the California Coast Range are being killed at an alarming rate by sudden oak death (SOD) (Meentemeyer et al. 2008), caused by the pathogen *Phytophthora ramorum* Werres, de Cock & Man in't Veld (Werres et al. 2001; Rizzo et al. 2002), with concerns being raised for the future of the species (Cobb et al. 2012; Cobb et al. this volume). This is particularly troubling as tanoaks are an important member of the California coastal forest ecosystem. Their acorns are an important food source for mammals and birds (Immel 2006), and their roots support a diverse community of fungi (Bergemann and Garbelotto 2006). However, the importance of tanoaks in the ecosystem has not always been acknowledged, and often it has been labeled as a “trash tree.” As a result, the majority of research on tanoaks has focused on how to kill it using herbicides (reviewed in Bowcutt 2011). Until recently, very little was known about tanoak phylogeography, breeding system, or population structure (Nettel et al. 2009; Dodd et al. 2013). Much is unknown about the basic biology of the species, including how pollen is moved from one

tree to another. Here we present data suggesting that tanoaks may also play an important role in supporting pollinator communities.

Pollen can be moved between trees in a number of ways including wind, insects, mammals, or birds (Proctor et al. 1996). Understanding how pollen is carried between flowers helps to shed light on a number of important features of the biology of a plant. How far does the pollen travel? What is the size of its genetic neighborhood? What is the expected genetic structure of the species? How should conservation reserves be designed?

Tanoaks have been generally assumed to be wind pollinated. They have always been closely associated with members of the true oaks (*Quercus* spp.) and were first attributed to the genus *Quercus* (reviewed in Bowcutt 2011). Tanoaks have flowers similar to most other oak species, which are indeed wind pollinated (Proctor et al. 1996), except that male inflorescences (aments) in tanoak are erect, similar to insect-pollinated chestnut aments. An ament contains many staminate (male) flowers, and can also contain pistillate (female) flowers at the base (Fig. 1). The idea that the flowers are wind pollinated has never before been tested.

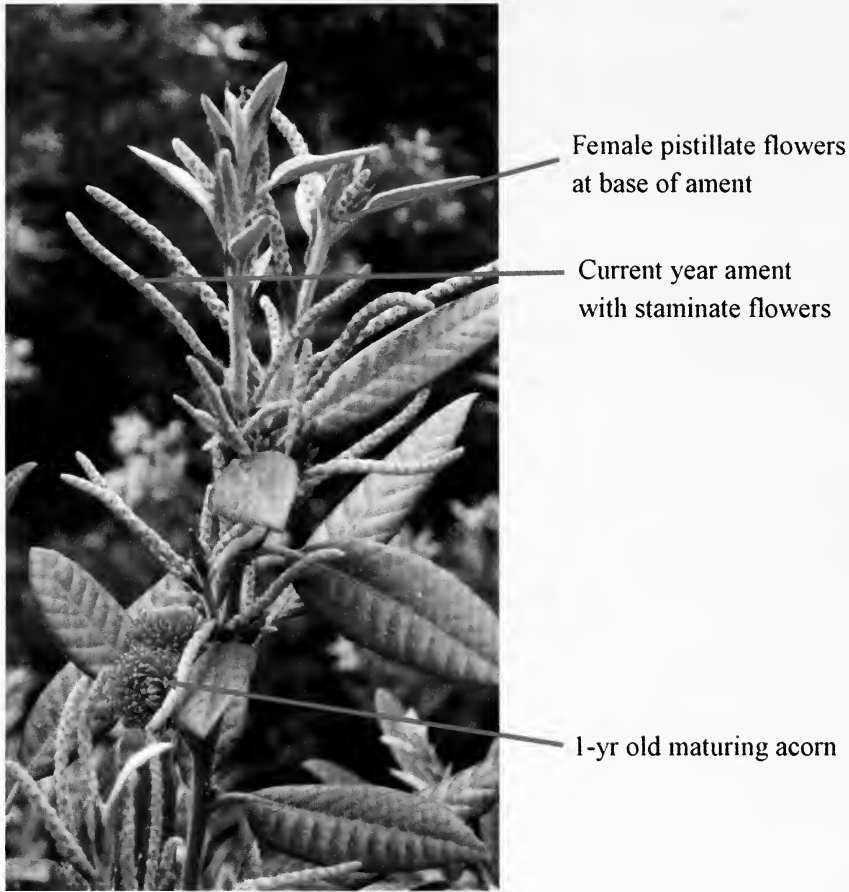


FIG. 1. A flowering branch from a tanoak tree at Blodgett Forest Research Station.

Many insect species are dependent on pollen as an important source of protein in their diet—particularly many bee species—irrespective of whether or not pollen is transferred from male to female flowers (pollination). If some insects rely on the flowers for pollen or nectar, then the role of tanoaks in the ecosystem has been underestimated, and the insect community will be impacted in ways not yet understood by the loss of tanoak trees due to SOD.

Here we present data from two complementary lines of investigation to address the following questions:

1. Do insects visit tanoak flowers in the field?
2. When insects are excluded from visiting flowers, do acorns still develop? How does insect exclusion impact selfing rates?

We took this two-pronged approach because observational studies are excellent at determining the community of insects that is visiting the flowers. However, they do not provide information on whether or not those visits result in pollen being transferred from one tree to another—i.e., whether or not pollination took place. In order to

determine that, it is necessary to exclude insects from flowers and determine if the rate of fruit set is similar with and without insect visitors.

METHODS

Insect Visitors

During July and August of 2009, a team of nine volunteer citizen scientists spent 11.5 hrs observing insect visitors to tanoak flowers at three sites in the Midpeninsula Regional Open Space District (MROSD): Windy Hill, Long Ridge, and El Corte de Madera Creek in San Mateo Co., California, an area heavily impacted by SOD. The volunteers were coordinated by MROSD staff and were given detailed written instructions on how to conduct the insect observations. Each volunteer recorded the following information: date; time; approximate temperature; and whether or not the focal flowers were in the sun, shade, or dappled light. They then selected a set of focal aments (from 1–36) consisting mainly of male flowers, which represented a group of flowers that they could comfortably watch all of during the observation

period. Each observation period lasted typically for 10 minutes. Each visit by an insect during the observation period was then recorded. A visit was defined as an insect coming into contact with the flower, and then departing. Sixty-five different observation periods were recorded. Volunteers were asked to categorize visitors as bees, flies, butterflies, beetles, ants, or birds. If they could not distinguish a visitor as a bee or a fly, they were asked to record it in a separate category: “bee/fly?”

Insect observations data analysis. To simplify the analyses and to account for non-random variation between observers, each observation period was assigned a “yes” or “no” value according to whether or not an insect visitor was observed (both for total visitors and by individual insect type). To summarize the data, stacked bar charts showing the frequency of each type of insect visitor were made. The charts do not contain error bars as they reflect observation counts made by the observers.

Flowering Phenology at the Blodgett Forest Research Station, Eldorado Co. (2009)

At a second field site in the foothills of the Sierra Nevada (an area uninfested by SOD), we observed bud, shoot, and flower development weekly throughout the flowering season, beginning in May 2009 and continuing through July 2009.

Floral-bagging Experiment and Insect-exclusion Experiment (2009)

At the Research Station, Eldorado Co., CA, we bagged five clusters of inflorescences on each of two branches per tree for 10 trees on June 1, 2009 (Fig. 2). Numbers of aments per cluster were variable. Bags were made from 1-mm mesh, wedding-veil material sewn closed and wrapped tightly around the branch to prevent insect entry. The mesh size was large enough to allow wind-blown pollen to enter (Neal and Anderson 2004). Although the mesh may have impeded some wind-blown pollen from entering, we expected ample pollen to be available because of the large number of tanoaks in the plot. The bags were tightly attached to the branches, but were loose around the inflorescences, so that damage to flowers or developing fruits is likely to have been minimal. At the same time we marked a similar number of inflorescences that were un-bagged, to serve as controls. On June 15, 2009, some of the male flowers were shedding pollen.

Bags were removed at the end of the flowering season in September 2009 and acorn development was observed in October 2010 after the two-year maturing period of tanoak acorns. Because the



Inflorescence in wedding veil

FIG. 2. An example of the pollinator exclusion bags excluding pollinators from visiting tanoak flowers.

numbers of pistillate aments varied among clusters of aments and the numbers of involucre per pistillate ament varied, we adjusted the observed numbers of acorns set for the observed numbers of pistillate aments per cluster and assumed an average of two involucre per pistillate ament. Differences in proportions of acorns set were tested with one-way analysis of variance, with bagging as the main factor and trees as replicates with branch data averaged per tree.

To test that these acorns were successfully pollinated, they were dissected to determine the presence of an embryonic plumule and radicle. A small piece of the cotyledon of each acorn was excised for DNA extraction. DNA of the cotyledons and foliage of mother trees was extracted and amplified using a set of nine microsatellite primers in order to determine whether the progeny were the result of selfing or outcrossing (for extraction and PCR protocols see Nettel et al. 2009).

Insect-exclusion and Emasculation Experiment (2010)

The bagging experiment that we performed in 2009 was intended to test whether tanoak flowers were predominantly insect pollinated. We genotyped acorns to assess selfing, but mutations and allele scoring errors could confound the results. Therefore, in this second study we repeated inflorescence bagging, but nested emasculation treatments within the bagging study. We bagged six clusters of inflorescences per tree for 20 trees on May 21, 2010. Male aments were removed

from three clusters per tree at the time of bagging, or as the aments extended. For combined pistillate–staminate aments, the distal staminate portion was removed. The remaining three clusters per tree were not emasculated to serve as controls of the effects of emasculation. In addition, we marked six clusters of inflorescences per tree that were un-bagged, three of which were emasculated and three of which were left intact. We removed the bags in October 2010, and acorn development was observed in October 2011. Differences in proportions of acorns set were tested with a two-way nested analysis of variance, with bagging as the main factor and emasculation nested within bagging and trees as replicates. Data were arcsine square-root transformed, by first taking the square root and then taking the arcsine of the square-root transformation.

A portion of the acorn cotyledon was excised for DNA extraction and amplification as for the 2009 experiment.

Estimating Selfing/Outcrossing

Because we had maternal genotypes for each of the acorns that were genotyped, and we had not genotyped potential paternal trees in the vicinity of the sample trees, we manually tested for evidence of outcrossing. Acorns were considered to be of outcross origin if at least one of the alleles at a locus was different than either of the alleles at that locus in the mother tree. We recognize that this does not account for potential mutations and allele scoring errors.

RESULTS

Insect Visitors

In 65 observation periods, spanning 11.5 hours, the citizen scientists observed 148 visits to tanoak flowers by insects. Long Ridge had the largest number of observation periods with at least one visitor recorded (20 periods, or 58.8% of observations) (Fig. 3a). However, Windy Hill had the highest percent of observation periods with visits (10 out of 15, or 66.7%). At Windy Hill, only bees and flies were observed, while all insect-visitor types were observed at Long Ridge (Fig. 3b).

Flowers located in the sun showed a trend towards a higher proportion of observation periods that recorded a visit compared to flowers in dappled light or shade (Fig. 4a). The temperature at the site (cool, warm, or hot) did not influence the proportion of observation periods with an insect visitor (Fig. 4b), nor did the time of day (morning vs. afternoon) (Fig. 4c). However, beetles were observed only in the afternoon (Fig. 5a). The part of the flowering season did not influence visitation (Fig. 4d), with the

exception of beetles, which were not observed towards the end of pollen shed (Fig. 5b).

Flowering Phenology at the Research Station

Inflorescences first appeared as the bud scales opened during the first week of May. At this stage, inflorescences were short and compact and took about 10 days to reach full size. The first inflorescences to expand were mostly exclusively pistillate. As the shoot continued to expand later in the season, combined pistillate and staminate inflorescences were formed. These combined inflorescences included: 1) a distal staminate ament that was a little shorter than the earlier staminate aments; and 2) 1–3 female flowers at the base. These later-season aments became fully expanded during the period in which the earlier staminate aments were still shedding pollen.

This double pattern of male flowering provides a broad period for pollen dispersal. We observed differences of as much as 18 days between the flowering phases in different trees in the population. This variation in phenology among trees means that female flowers for an early-flowering individual are likely to be pollinated from the early staminate flowers, whereas late-flowering individuals could still be pollinated from the combined pistillate–staminate aments. In general, the two phases of staminate ament production provide an extended period of pollen shedding, so that most female flowers have a strong likelihood of being pollinated.

Insect-exclusion Experiment (2009)

Because the numbers of pistillate aments varied among clusters of aments and the numbers of involucre per pistillate ament varied, we adjusted the observed numbers of acorns set for the observed numbers of pistillate aments per cluster and assumed an average of two involucre per pistillate ament. Differences in the proportion of acorns set were highly significant ($P < 0.001$). About 14% of involucre in bagged inflorescences produced fully swollen acorns by October 2011, compared to 65% of unbagged inflorescences (Table 1). These data indicate that 1) the proportion of successful pollinations per inflorescence was lower when insects were excluded; and 2) some flowers from which insects were excluded were fertilized, presumably either from self-pollen or wind-blown pollen penetrating the veil.

Insect-exclusion Experiment (2010)

As in the first experiment, bagging to exclude insects resulted in a lower rate of acorn set ($P < 0.001$), but did not prevent pollination entirely (Table 2). Emasculation resulted in reduced acorn set in both bagged and unbagged tests (P

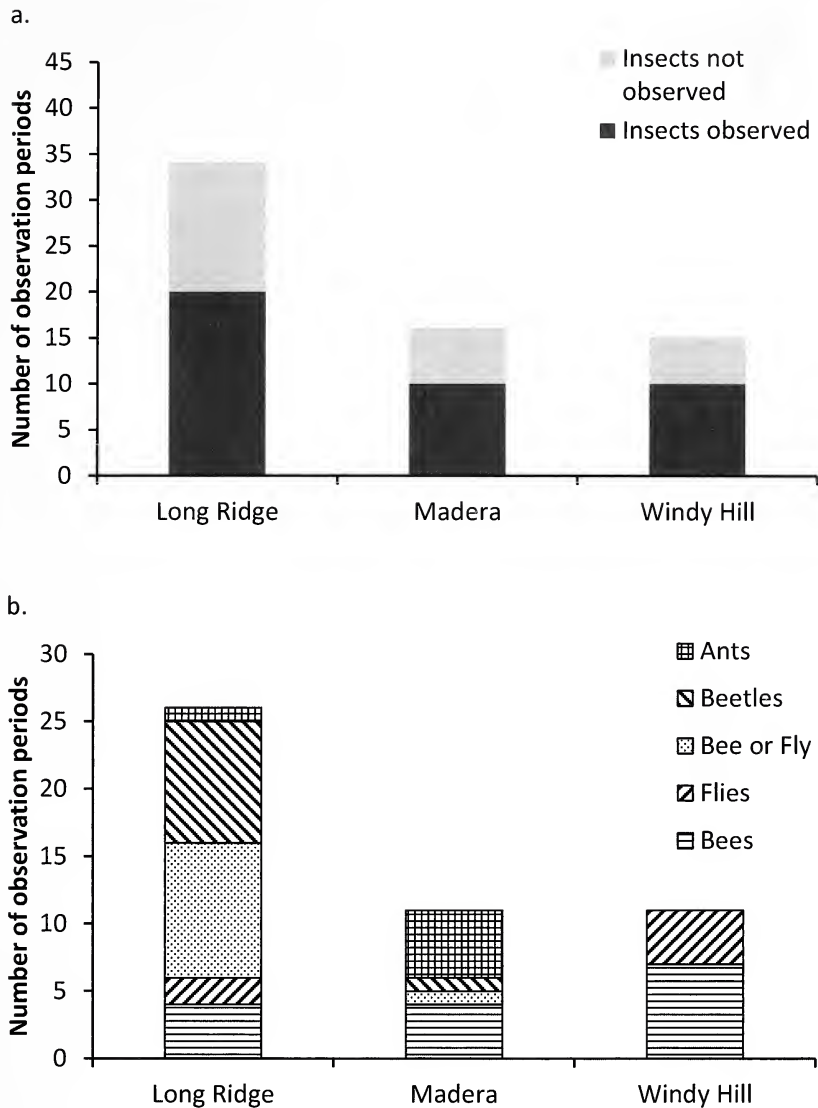


FIG. 3. 3a, total number of observation periods made at each site partitioned by whether or not insects were observed during each observation period; 3b, the number of observation periods at each site in which each of the four types of insect visitors were observed.

< 0.001). However, the relative effect of emasculation was greater in the bagged experiment than in the unbagged, suggesting pollen limitation because of the veil.

As expected, we did not detect any selfing among the bagged, emasculated inflorescences. However, a low proportion of selfed seeds were detected in the bagged, intact and in the unbagged, emasculated treatments (Table 2). The latter could be the result of geitogamous matings (pollen from other flowers on the tree). In total, three acorns were classed as selfed in the bagged, intact treatment and a single acorn was classed as selfed in the un-bagged, emasculated treatment.

DISCUSSION

Tanoaks have been assumed to be wind-pollinated. Our data suggest that 1) tanoak is primarily an insect-pollinated species; and 2) some level of wind pollination is also possible.

These results could have important consequences for ecological conservation that need further investigation, both from the perspective of the insects and the trees. There could be a community of insects that are dependent on tanoaks as a food source, and the future reproduction of tanoaks could be somewhat dependent on those insects.

Pertaining to insect biology, it is first necessary to consider what the data do and do not show.

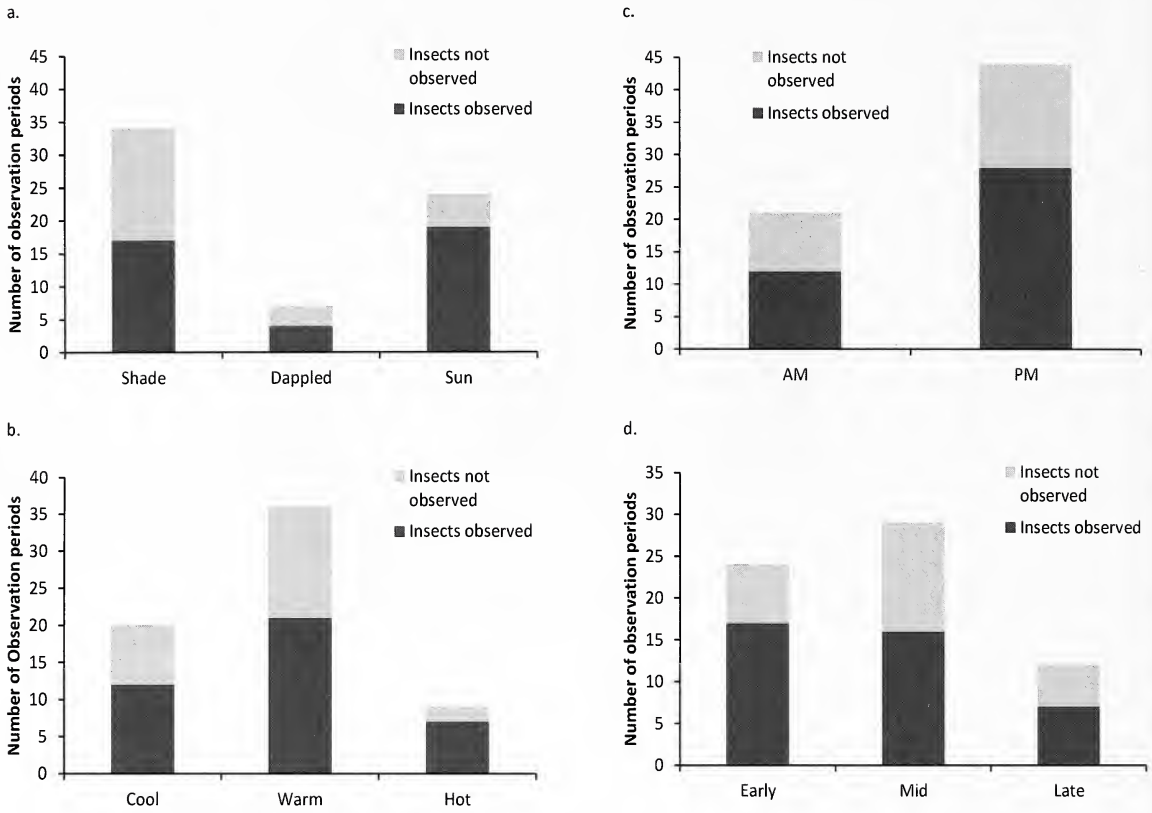


FIG. 4. Total number of observation periods in different environments; 4a, with flowers in each of the three different qualities of light: full shade, dappled light, or full sun; 4b, at three different temperature conditions: Cool $\leq 75^{\circ}\text{F}$, Warm = $75\text{--}85^{\circ}\text{F}$, Hot $\geq 85^{\circ}\text{F}$; 4c, in the morning or afternoon; and 4d, over the course of the flowering season: Early = July 1–July 15, 2009, Mid = July 16–July 31, 2009, Late = August 1–August 15, 2009.

While the data do show that insects visit tanoak flowers, they do not show what the importance of tanoak pollen is in their diet. Moreover, the community of insects has not yet been characterized. How many different species use tanoak flowers? How many of those species are native? (Several non-native honeybees were observed in this study.) These questions are relevant for determining the importance of tanoaks for the native pollinator community, and thus the impacts that SOD would have if some areas become extirpated of tanoaks.

For trees, these results have some very clear implications for conservation, particularly in light of SOD. The movement of pollen across the landscape is an area of very active research (Austerlitz et al. 2004; Robledo-Arnuncio et al. 2006) that recently has overturned some of the classical paradigms of mainly local matings (Ashley 2010) and expected lower genetic diversity in fragmented populations (Kramer et al. 2008). Many studies have shown that the dispersal kernel is fat-tailed and some pollen can travel great distances—whether it be wind-pollinated as in Scots pine (*Pinus sylvestris* L.), in which pollen has been recorded to have traveled

and caused effective pollination over distances exceeding 100 km (Robledo-Arnuncio 2011), or insect-dispersed pollen over 160 km as in *Ficus sycomorus* L. (Ahmed et al. 2009). Indeed, fragmentation in many cases has only minor or non-significant effects on genetic diversity because of long-distance pollen dispersal (Kramer et al. 2008). However, the degree of fragmentation and the distance between fragments are likely to play a crucial role in individual cases and will be important in conservation of tanoak following disease epidemics. Although the dispersal kernel of pollen is important in the underlying ability to effect long-distance fertilizations, local matings are likely to result in genetic neighborhoods that will have important consequences on the selection of seed trees for replanting (Dodd et al. 2013).

In fragmented habitats, the size of the genetic neighborhood—and the distance traveled by pollen—can become increasingly important, as pollen must move between fragments in order to prevent a loss of genetic diversity in the remnant fragments (Ellstrand 1992; Kramer et al. 2008). In some areas tanoak populations are being decimated by SOD, and as such, are rapidly

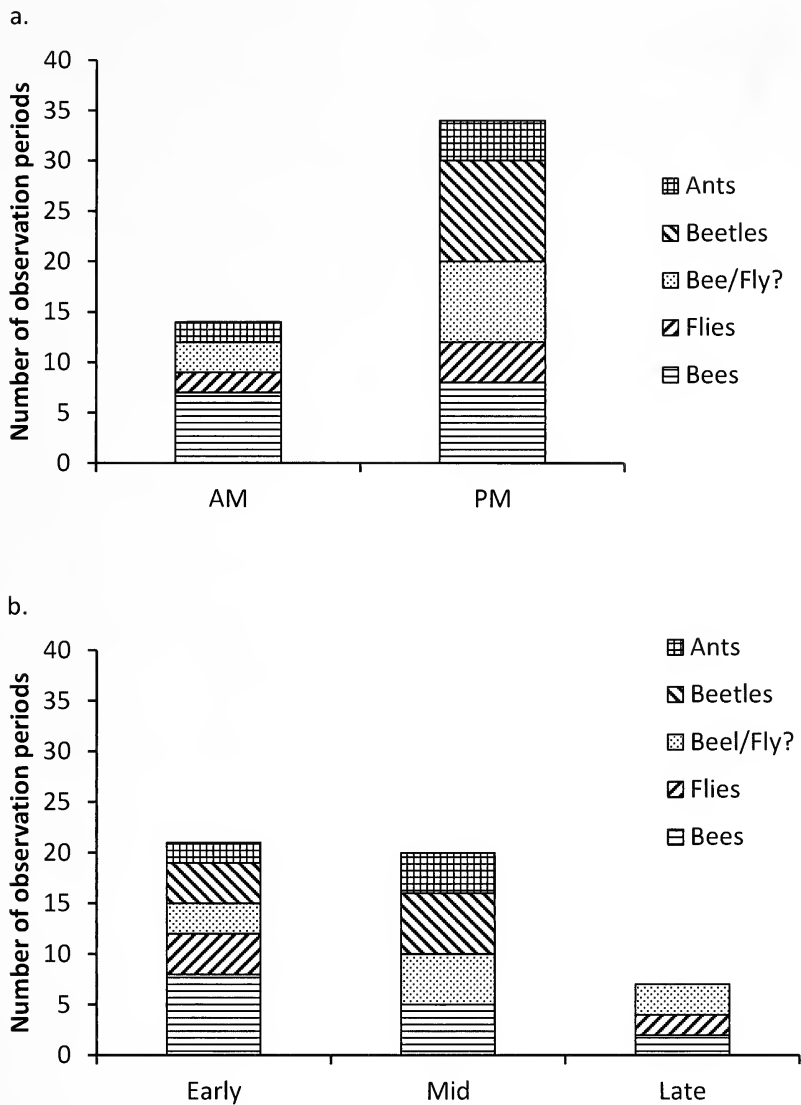


FIG. 5. The number of observation periods in which each of the four types of insect visitors were observed; 5a, in the morning or afternoon; 5b, over the course of the flowering season: Early = July 1–July 15, 2009, Mid = July 16–July 31, 2009, Late = August 1–August 15, 2009.

changing their patterns of fragmentation as populations split or steeply decline. Knowing that tanoaks rely on insect pollinators is critical to understanding the consequences of this recent fragmentation; should the distance between fragments exceed the flight distances of pollinating

insects, loss of genetic diversity could be an important consequence. Further information that would be useful for informing conservation planning for surviving tanoak populations includes knowing the distance that pollen moves between individual trees

TABLE 1. ACORN SET IN BAGGED INFLORESCENCES TO EXCLUDE INSECTS AND OPEN-POLLINATED (UNBAGGED) INFLORESCENCES IN 2009 EXPERIMENT. (Standard errors in parentheses.)

Treatment	Mean number of pistillate aments per cluster	Mean number of acorns set per cluster	Mean proportion of acorns set per cluster assuming two involucre per pistillate ament	Mean proportion of acorns set that were selfed per cluster
Bagged	6.3 (0.2)	1.78 (0.2)	0.14	0.02 (0.01)
Unbagged	7.1 (0.8)	9.24 (1.2)	0.65	0.04 (0.02)

TABLE 2. ACORN SET IN BAGGED INFLORESCENCES EMASCULATED AND INTACT TO EXCLUDE INSECTS AND OPEN-POLLINATED (UNBAGGED) INFLORESCENCES IN 2010 EXPERIMENT. (Standard errors in parentheses.)

Treatment	Mean number of pistillate aments per cluster	Mean number of acorns set per cluster (October 2012)	Mean proportion of acorns set per cluster assuming two involucre per pistillate ament	Mean proportion of acorns set that were selfed per cluster
Bagged (emasculated)	5.1 (1.7)	0.7 (0.08)	0.05 (0.005)	0
Bagged (intact)	7.6 (1.9)	1.6 (0.19)	0.11 (0.01)	0.02 (0.01)
Unbagged (emasculated)	7.2 (2.1)	7.2 (0.34)	0.50 (0.02)	0
Unbagged (intact)	6.5 (2.0)	11.7 (0.34)	0.77 (0.02)	0.002 (0.002)

and populations. What are the flight distances of the insects that pollinate them? Moreover, information on the composition of the pollinator community is critical, as conservation planning also needs to account for maintaining the populations of insects that visit tanoak flowers in order to assure maximum seed set.

ACKNOWLEDGMENTS

The authors would like to thank Neal Williams, UC Davis and all of the citizen-scientist volunteers and Cindy Roessler as well as the Midpeninsula Regional Open Space District for making this project possible. This research was funded by the USDA-Forest Service Pacific Southwest Research Station Sudden Oak Death Research Program.

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IMPLICATIONS OF TANOAK DECLINE IN FORESTS IMPACTED BY
PHYTOPHTHORA RAMORUM: GIRDLING DECREASES THE SOIL HYPHAL
ABUNDANCE OF ECTOMYCORRHIZAL FUNGI ASSOCIATED WITH
NOTHOLITHOCARPUS DENSIFLORUS

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ABSTRACT

Invasive plant pathogens are often recognized as serious threats to the maintenance of biodiversity affecting both structure and function of ecosystems. Here, we investigate the potential impact of the invasive pathogen *Phytophthora ramorum* Werres, de Cock & Man in't Veld by using physical girdling of tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), as a surrogate for the disease and to test for changes on the hyphal abundance of ectomycorrhizal fungi. In this study, the flow of phloem to the roots of girdled trees was severed by cutting two narrow incisions (about 10 cm distant) through the inner bark around the circumference of the stem of each tree (fully-girdled), or by cutting two narrow incisions half of the circumference of the tree (half-girdled), to compare with untreated (non-girdled) trees. The hyphal abundance of two common and ecologically important ectomycorrhizal genera (*Cenococcum* and *Tricholoma*) was estimated from the roots and surrounding soil using real-time PCR quantification (TaqMan) assay. A significant decrease in the hyphal abundance from soil was observed in girdled tree plots. In contrast, no similar decrease in the root hyphal abundance was observed. Ectomycorrhizal fungi have a major impact on ecosystem function through their control over decomposition, nutrient acquisition, and mobilization and regulation of succession in plant communities. Given their important function, the decline in EM abundance of tanoak infected by *P. ramorum* will likely disrupt the function and structure of these forests.

Key Words: Ectomycorrhiza, extramatrical mycelium, girdling, *Phytophthora ramorum*, sudden oak death, tanoak.

The dissemination and spread of invasive plant pathogens has increased dramatically over the last century as a result of the inadvertent movement of infected plants (Pimentel et al. 2000; Liebhold et al. 2012). One recent invasion involves the introduction of the microbial pathogen, *Phytophthora ramorum* Werres, de Cock & Man in't Veld, the cause of the disease referred to as Sudden Oak Death or SOD. The pathogen often appears as a lethal canker on tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh, and a few oak species: *Quercus agrifolia* Née, *Q. kelloggii* Newb. and *Q. parvula* Greene (all in the Fagaceae), in the central coastal region of California (Garbelotto et al. 2001; Rizzo et al. 2002). Although the origin of *P. ramorum* in forests is unknown, the disease was likely introduced in central California on infected nursery stock and dispersed long

distance by the transport of infected plants or locally by wind-blown rain (Davidson et al. 2005; Ivors et al. 2006; Mascheretti et al. 2008; Grünwald et al. 2012). In mixed-evergreen and redwood–tanoak forests of the central coast of California, *P. ramorum* has reached epidemic levels, aided by its rapid sporulation on non-lethal hosts, especially bay laurel, *Umbellularia californica* (Hook. & Arn.) Nutt., during rainy intervals (Davidson et al. 2005). By far, tanoak is the most susceptible host as evidenced by the high recovery of *P. ramorum* from lethal cankers, the thousands of dead tanoak trees observed in coastal forests, and the lack of genetic resistance within tanoak populations (Davidson et al. 2005; Waring and O'Hara 2008; Hayden et al. 2011).

Tanoak, a broadleaf evergreen tree, is a significant component of the low- to mid-canopy strata of mixed-evergreen and coast redwood, *Sequoia sempervirens* Endl., forests in central California and southern Oregon (Waring and O'Hara 2008; Ramage and O'Hara 2010; Ramage et al. 2011). In redwood forests, tanoak is often the dominant

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ectomycorrhizal (EM) host, forming obligate associations with a diverse assemblage of fungi (Kennedy et al. 2003; Bergemann and Garbelotto 2006). This mutualism involves the direct mobilization and translocation of nutrients (especially N and P) from fungi in exchange for carbon derived from plant photosynthesis (see review by Leake et al. 2004). In a survey of mature (ca. 60 yr) tanoak roots in mixed Douglas-fir–tanoak forests in northern California, over 250 species of root-associated fungi were estimated from a 2-km² area (Bergemann and Garbelotto 2006). The vast majority of root-associated fungi shared affinity with well-known EM fungi of the Ascomycota and Basidiomycota (dominant fungi include *Cenococcum geophilum* Fr., and species of *Russula*, *Lactarius*, and *Tomentella*) (Bergemann and Garbelotto 2006).

EM fungi are of major importance in microbial communities because of their role in plant-nutrient acquisition and regulation of succession in plant communities (Nara and Hogetsu 2004; Nara 2006). Given their role, the question arises as to what will be the impacts of infection by *P. ramorum* on tanoak EM composition and function? The decline of EM function is likely to be more pronounced in forests where tanoak is the dominant EM host (e.g., tanoak–redwood forests) because of the reduced EM inoculum. In contrast, other EM hosts may counter the effects of declining abundance if they have similar EM assemblages. In tanoak–Douglas-fir forests, the majority of EM species found on the roots of tanoak seedlings were also found on Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (Kennedy et al. 2003). In contrast, coast redwood forms associations with arbuscular mycorrhizal (AM) fungi, including species in the Glomeromycota (Wang and Qiu 2006), and ericaceous shrubs form assemblages with a different assemblage of fungi. Although AM, EM, and ericoid mycorrhizae are able to mobilize and transfer N and P, the enzymatic capabilities of EM allow for greater N acquisition by hydrolysis of organic polymers in litter and soil (Read and Perez-Moreno 2003; Talbot and Treseder 2010).

The objectives of this study are to simulate the mortality caused by *P. ramorum* through physical girdling of trees and assess the EM biomass from roots and soil. Because of the dependence of carbon assimilate from the tanoak trees to fuel the growth and activity of EM fungi, it would be expected that girdling should decrease the EM biomass of roots and soil in plots with girdled trees. Here, we test this hypothesis using a quantitative PCR (qPCR) assay to target hyphae of EM fungi from tanoak roots and the surrounding soil. Due to the complexity of the EM assemblage in the Douglas-fir–tanoak forest (Kennedy et al. 2003; Bergemann and Garbelotto 2006), we focus on sampling two EM genera (*Cenococcum* and

Tricholoma) that vary with respect to reproduction (asexual or sexual), extramatrical hyphal abundance, and their prevalence in the tanoak root community. *Cenococcum geophilum* is the most frequently encountered taxon in tanoak (Kennedy et al. 2003; Bergemann and Garbelotto 2006). The mycelia of *C. geophilum* are considered a short-range exploration type due to the short hyphal extensions observed on EM roots (Agerer 2001). In contrast, *Tricholoma* species maintain extensive aggregates of mycelium that may be connected to medium-distance transport structures called cords (Agerer 2001). Here, we compare the abundance of the two genera from both substrates after disruption of the carbon flow from leaves to roots by girdling trees.

MATERIALS AND METHODS

Study Site, Experimental Design, and Sampling

The study was conducted on privately owned Douglas-fir–tanoak forest near the town of Whitethorn, California (Humboldt Co.), USA (40°00'30"N, 123°57'00"W) (Fig. 1A). The selection of non-girdled and girdled (half-girdled and fully-girdled) followed a partially randomized block design. Five blocks (1600 m²) were chosen on the basis of similar densities of tanoak and the absence of Douglas-fir and ericoid trees or shrubs (*Gaultheria shallon* Pursh, *Vaccinium ovatum* Pursh (Fig. 1B). Baseline sampling was performed to examine EM composition prior to girdling in January 2003 (Bergemann and Garbelotto 2006). Next, non-girdled tree plots were assigned to the center of each of the five blocks in an attempt to balance the intrusion of living roots into treated plots (Fig. 1C). The remaining two treatments (half-girdled and fully-girdled) were randomly assigned to the two plots within each block (Fig. 1C). The phloem of girdled trees was severed with a chainsaw by cutting two narrow incisions (about 2 cm in depth and 10 cm distant) around the circumference of the stem of each tree (fully-girdled) or by cutting two narrow incisions half of the circumference of the tree (half-girdled) for comparison with non-girdled trees. Half-girdling (girdling half the circumference of the tree) was performed to determine whether the reduction of carbon assimilate exhibited properties of similar severity under a partial flux in the phloem. Root tips and soil were sampled from each plot, five (June 2003), nine (October 2003), and 13 (February 2004) months after girdling. Two, 6-m, perpendicular transects were placed by random selection of two intersecting points along 15 m × 15 m grids positioned in the center of each plot (Fig. 1D). Three soil cores were sampled at 2-m intervals (n = 6) along each transect from each plot (n = 15) (Fig. 1D), using PVC pipe 20 cm in length with an internal

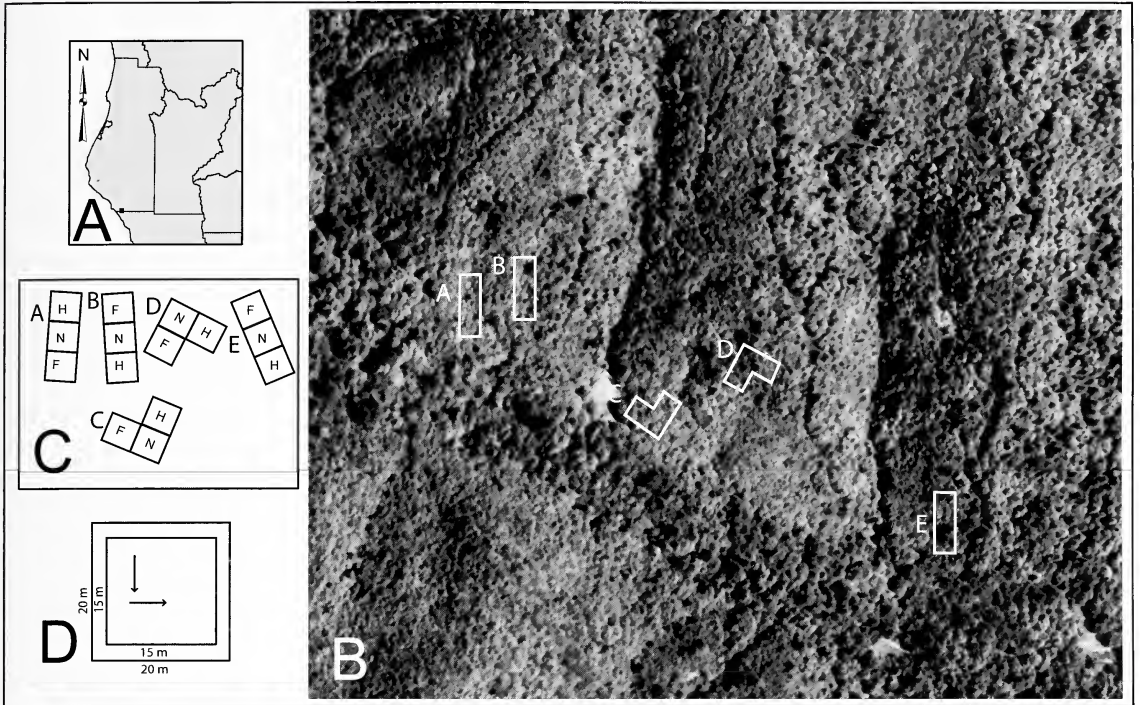


FIG. 1. Location of tanoak study sites and experimental block layout. A. Location of the study site in southern Humboldt County, California. B. Aerial photograph showing the location of blocks. C. Experimental layout of each block after simple randomization of treatments. Control plots were positioned in the center of each block and experimental plots (N = 'non-girdled', F = 'fully-girdled', H = 'half-girdled') were randomly assigned. D. Layout of plot design showing the grid method used for establishing two, 6 m transects for collecting soil and roots positioned towards the center of the plot.

diameter of 2.5 cm and transported on ice to the lab at UC Berkeley within 48 hr. Each core was divided into 10 sections of equal volume (each 16 cm³), and two subsections were randomly selected from the 10 subsections using simple random number generation and excised using an electric saw. Soil cores were stored at 4°C until processed. Soil and roots were lyophilized for approximately 36 hr, after which all fine root mass (<2 mm in diameter) was separated from soils using a forceps, then weighed and stored at -80°C.

Quantification of Ectomycorrhizal Abundance Using TaqMan Assays

The gene amplified from *Cenococcum* and *Tricholoma* in TaqMan assays was the nuclear ribosomal large subunit DNA (28S nrDNA), and the conserved regions for primer design were based on alignments of EM sequences generated for phylogenetic analysis of tanoak EM communities (Bergemann and Garbelotto 2006). Primers and probes were designed using Primer 3 ver. 0.6 (Rosen and Skaletsky 2000) with the following parameters: 1) product size 50–90 bp; 2) primer size = 18–27 bp; 3) primer T_m = 58–60°C; 4)

Max primer T_m difference = 2; 5) hybrid oligo size = 21–30 bp; 6) hybrid oligo T_m = 67–70°C (Table 1). Primers and dual labeled probes with a 5' fluorophore (6FAM) and 3' black hole quencher (BHQ) were synthesized by Operon (Huntsville, AL) (Table 1).

Genomic DNAs were extracted from pooled root sections and 10% of the soil mass was subsampled using the UltraClean Soil DNA Kit (Mo Bio Laboratories, Carlsbad, CA) following the manufacturer's recommendations. DNA quantity and detection was measured using the 5' fluorogenic exonuclease (TaqMan) qPCR assay that combines the use of an internal probe with standard PCR primers (Heid et al. 1996). The probe is labeled with a 5' fluorescent reporter dye and a 3' quencher molecule. Once the reporter is bound and the *Taq* enzyme elongates the target sequence, the reporter dye is released and fluorescence is detected (Heid et al. 1996). Two standards, for *Cenococcum* (N72) and *Tricholoma* (S1) shown in Table 1, were generated for standard quantification by 10-fold serial dilution (10^{-1} – 10^{-5} pg) after purification of plasmid DNA (Qiagen Plasmid Mini-Prep, Valencia, CA). The quantity of DNA was estimated using a UV spectrophotometer (Bio-Rad, Hercules, CA). To

TABLE 1. SEQUENCE IDENTIFIERS, GENBANK ACCESSIONS, TAQMAN PRIMERS, AND PROBES AND CHARACTERISTICS OF TWO ECTOMYCORRHIZAL GENERA (*CENOCOCUM* AND *TRICHOLOMA*) QUANTIFIED IN GIRDLING EXPERIMENTS. References: 1) Massicotte and Trappe 1992; 2) Shinohara et al. 1999; 3) Gill et al. 2000; 4) Agerer 2001; 5) Jany et al. 2002; 6) Huai et al. 2003; 7) Chapela and Garbelotto 2004; 8) Douhan and Rizzo 2005; 9) Gryta et al. 2006; 10) Carriconde et al. 2008b; 11) Carriconde et al. 2008a; 12) Jargeat et al. 2010; 13) Grubisha et al. 2012.

Genus	Species composition	Sequence identifier and GenBank accession numbers	Primer and probe sequences (5'-3')	Genetics, morphology, reproduction
<i>Cenococcum</i>	22 ITS sequence types	P62 - DQ273447	Cen F: CCAGCATC-CTAGCCGAAG	<i>Reproduction</i> —no known sexual stage, form sclerotia (1) <i>Morphology of EM</i> —smooth, thick mantles with short-emanating hyphae, no rhizomorphs (4) <i>Dispersal of clerotia</i> —water, birds, insects, human-mediated transport of plants, rodents (2) <i>Distribution</i> —widespread, all continents (2) <i>Genetic diversity</i> —genotypic diversity high in populations studied (5, 8); some form cryptic species (8) <i>Reproduction</i> —sexual, epigeous sporocarps (6) <i>Morphology of EM</i> —undifferentiated to smooth mantle, some with cords (3); <i>T. magnivalere</i> and close allies form dense hyphal mats (shiros) (7); well-developed extramatrical mycelia observed in several species (4) <i>Dispersal</i> —spores in epigeous fruit bodies (7) <i>Distribution</i> —widespread, continental (1, 7) <i>Genetic diversity</i> —many genets in some species (2, 6, 10); few genets in some species (9); some form cryptic species (11, 12, 13)
		A27 - DQ273448	Cen Hyb: GGACCTCA-GTTCAGGCTGGCC	
		F39 - DQ273449	Cen R: GTTATAGC-CCGTGCGAAAT	
		A4 - DQ273450		
		N78 - DQ273451 N72 - DQ473308		
<i>Tricholoma</i>	<i>T. magnivalere</i>	G58 - DQ273556	Trich F: CGGACTACC-AGGCTTATG	
	<i>T. saptonaceum</i>	R24 - DQ273557	Trich Hyb: GCGCTCTCAA-AGAGTCGAGTGTGTTG	
<i>T. portentosum</i>		F16 - DQ273558	Trich R: CCCATTAGAG-CTGCATTCC	
	<i>Tricholoma</i> sp. 1	S1 - DQ273559		
	<i>Tricholoma</i> sp. 2	W74 - DQ273560		

TABLE 2. OPTIMIZED PARAMETERS FOR QUANTITATIVE TAQMAN ASSAYS OF *CENOCOCCUM* AND *TRICHOLOMA*.

Genus	T _a 56–62°C	Primer concentration	Probe concentration/ label	Root template	Soil template
<i>Cenococcum</i>	58°C	260 nM	260 nM/6FAM	1:1000	1:5000
<i>Tricholoma</i>	57°C	200 nM	260 nM/6FAM	1:100	1:1000

test the specificity of the TaqMan primers and probes, all plasmids with target 28S sequences from each genus were diluted (1:5000) and PCR amplified (Table 1). Next, we assessed whether the primers and probes would amplify non-target EM fungi after dilution within the quantified range of standards (5×10^{-5}) (Appendix 1). All TaqMan reactions were performed in a 15 μ l volume containing 1 \times TaqMan Universal Master Mix (ABI, Foster City, CA), 200–260 nm of forward and reverse primers, 260 nM dual-labeled probes and 5 μ l of template DNA diluted 1:100 to 1:5000 (Table 2). In the absence of cross reactivity, DNA template quantities were estimated using the MyiQ (6FAM) Real-Time PCR Detection System (Hercules, CA) with a single cycling parameter. Cycling conditions were as follows: 1 cycle at 50°C for 10 min, 1 cycle at 95°C for 1 min 30 sec, 55 cycles at 95°C for 15 sec and T_a for 1 min (Table 2), followed by a hold at 4°C for 30 sec. Standard DNA was quantified within the range of 5×10^{-1} – 5×10^{-5} pg for both *Cenococcum* and *Tricholoma*. Root and soil DNA templates were optimized for template quantity (i.e., diluted within the quantified range of the standards), and PCR efficiency (Table 2). To account for error in enzyme kinetics between the roots and soil, an environmental negative (either root or soil DNA extract with no target template) was added to the standards using the same dilution factor of the PCRs (Table 2). Threshold (C_t) values (the level at which template fluorescence exceeds background fluorescence) were calculated for each TaqMan assay using BioRad MyiQ Real-Time Detection System software using the maximum correlation coefficient approach (Hercules, CA). With this approach, the threshold is automatically determined to obtain the highest possible correlation coefficient for the standard curve under environmental PCR conditions. The standard curve was used to estimate the sample quantity of DNA from roots and soil DNA using the same software described above. If samples displayed irregular curvatures during the amplification cycles, they were removed prior to calculation of starting quantity.

The qPCR approach was to amplify fungal-specific hyphal abundance of *Cenococcum* and *Tricholoma* with separate reactions with separate primers from genomic DNA and to calculate hyphal biomass per sample by quantifying the concentration of starting DNA (pg) divided by the dry weight (g) of root and soil and multiplied by an appropriate dilution factor. After pooling

biomass of both sections from a single core (by summation of the biomass quantities from each section), a repeated measures ANOVA (using three-way RM-GLM with time sampled as within factor) was used to analyze the effects of the girdling in time on log (Y+1) transformed values of EM abundance of each taxon (*Cenococcum* and *Tricholoma*) from root and soil. If Mauchly’s criterion indicated rejection of the compound symmetry assumption (i.e., the lack of independence between the subject factor and the treatment), probability values were estimated after adjusting the number of the degrees of freedom for the F distribution using the Greenhouse–Geiser correction. Analyses were conducted using SPSS 17 (Chicago, IL) and considered significant at $P < 0.05$.

RESULTS

The repeated-measures analysis showed a significant reduction of EM soil hyphal biomass in girdled treatments (fully-girdled, half-girdled) compared to the control (non-girdled) (Table 3, Fig. 2). In contrast, we observed no significant reduction of EM root hyphal biomass in girdled plots (Table 3, Fig. 2). Additionally, EM soil hyphal biomass varied among sampling periods with greater soil hyphal biomass in early summer (June) compared to both the early fall (October) and late winter (February) sampling periods (Table 3, Fig. 2). EM root hyphal biomass also varied across seasons but a significant interaction between taxon and time indicates that seasonal variation is dependent on the taxa (Table 3, Fig. 3).

DISCUSSION

The main objective of this study was to determine whether reducing carbon flow from the leaves to the roots by girdling would cause a decline in the EM hyphal abundance. Our study demonstrates that the extramatrical hyphae of tanoak roots decrease in abundance after carbon depletion by girdling, whereas the root hyphal biomass is unaffected over the same duration of sampling. Our results are consistent with previous experiments that showed that a reduction of carbon assimilate from the leaves to the root by girdling resulted in a significant decline in the activity and biomass of soil microbes, mainly due to the loss of EM fungi (Högberg et al. 2001; Högberg and Högberg 2002; Göttlicher et al.

TABLE 3. RESULTS OF THE REPEATED MEASURES ANOVA. T = time of sample (five, nine and 13 months after girdling. F values and significance levels from the repeated measures ANOVA are shown for all main effects and their interactions: *0.01 < P < 0.05, **0.001 < P < 0.01, ***P < 0.001, ns = non significant. When Mauchly's P < 0.05, Greenhouse–Geisser estimates were used to correct for sphericity.

	Mauchly's P	Repeated measures GLM							
		T		T × Taxon		T × Treatment		T × Taxon × Treatment	
		F	P	F	P	F	P	F	P
root hyphal abundance (pg DNA g ⁻¹ root)	0.015	16.706	***	5.532	**	0.987	ns	0.912	ns
Taxon		41.417	***						
Treatment		0.792	ns						
Taxon × Treatment		0.594	ns						
soil hyphal abundance (pg DNA g ⁻¹ soil)	0.019	5.749	**	2.165	ns	0.124	ns	0.546	ns
Taxon		118.680	***						
Treatment		3.736	*						
Taxon × Treatment		0.932	ns						

2006; Scott-Denton et al. 2006; Weintraub et al. 2007; Feng et al. 2009; Kaiser et al. 2010). This study lends further support that girdling severely limits the growth and maintenance of the extramatrical hyphae, the main conduit for decomposition and nutrient acquisition and mobilization (Leake et al. 2004).

Microcosm and field studies of EM fungi have shown that up to 20–30% of net photosynthate is transferred to the fungal associate to support their growth and activity of the extramatrical mycelium (Söderström 1992; Högborg and Högborg 2002; Hobbie 2006). Furthermore, the extramatrical mycelia account for up to 80% of the total EM biomass and nearly 30% of the microbial biomass in temperate forests (Wallander et al. 2001; Högborg and Högborg 2002). Such an investment in the maintenance of these extensive mycelial networks is required for nutrient acquisition and mobilization (Leake et al. 2004). Here, the disruption of a carbon supply to the roots by girdling reduced the soil EM extramatrical mycelium.

Many EM species possess a broad class of the enzymes for acquisition and uptake of N and P from organic polymers (Read and Perez-Moreno 2003; Leake et al. 2004; Courty et al. 2010; Talbot and Treseder 2010). With the loss of a direct source of carbon assimilate from the host and after girdling, the enzymatic activity of proteases and cellulases show similar decreases (Kaiser et al. 2010). Cellulases are a suite of enzymes that enhance degradation of cellulose allowing entry of hyphae into plant litter (a feature typical of saprotrophic fungi). In general, EM fungi possess a reduced set of genes encoding cellulose-degrading enzymes (Martin et al. 2008; Nagendran et al. 2009; Wolfe et al. 2012) that contribute to poor cellulose degradation compared to that of saprotrophic fungi (Baldrian 2009). Rather, the decrease in the activities of cellulases is likely due to

the elimination of rhizosphere carbon inputs from the roots of girdled trees (Subke et al. 2004; Kaiser et al. 2010). In contrast, decreases in the abundant EM extracellular proteinases that hydrolyze proteins found in organic matter after girdling are a likely consequence of a decline in the abundance of EM soil extramatrical mycelia (Read and Perez-Moreno 2003; Talbot and Treseder 2010).

Although soil EM hyphal abundance was lower in girdled trees, we observed no similar decrease in EM hyphal root abundance after 13 months. Roots are known to be essential for the storage of starch used by EM and plants in the absence of a supply of carbon assimilate from the leaves (Pena et al. 2010). Such reserves are seasonally dependent; the depletion of starch reserves that occurs during spring bud break and the repletion during winter months of plant dormancy are common occurrences (Regier et al. 2010). In girdled trees, starch reserves are typically depleted over time (Bhupinderpal-Singh et al. 2003; Pena et al. 2010; Regier et al. 2010). For example, Pena et al. (2010) measured starch concentrations in the fine roots of girdled *Fagus sylvatica* L. trees and found quantities to be about one-quarter of that estimated from the roots of non-girdled trees. After two years, the roots of girdled *P. sylvestris* trees, soluble carbohydrates were reduced to a small fraction of that found in non-girdled trees (Bhupinderpal-Singh et al. 2003).

We found no significant differences in EM abundance between girdled (half-girdled and fully-girdled) and non-girdled trees. One possible explanation for this result is that the transport of carbon from the leaves to roots is maintained in fully-girdled trees near levels of half-girdled trees. In *F. sylvatica*, a low supply of carbon assimilate bypasses the girdle through transport in axial parenchyma cells, yet these fractions are insignif-

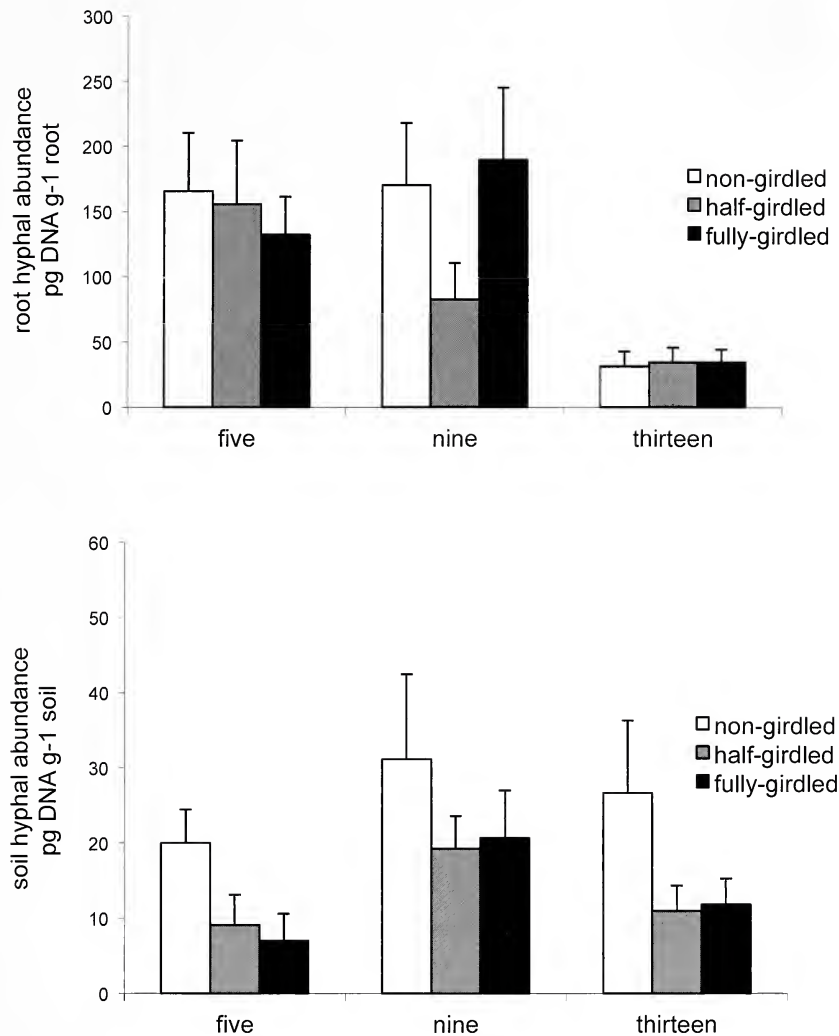


FIG. 2. Ectomycorrhizal hyphal abundance from roots and soil five (June 2003), nine (October 2003) and thirteen (February 2004) months after girdling *Notholithocarpus densiflorus* trees. Mean hyphal abundance for each treatment (+1 SE) are graphed. Girdling decreased the ectomycorrhizal soil hyphal abundance did not similarly affect root hyphal abundance.

icant for supporting the EM mycelia of roots (Druebert et al. 2009). Therefore, a more plausible explanation for the similar decline in EM soil hyphae in girdled trees is that carbon resources after girdling are directed towards secondary metabolic pathways (e.g., production of phenolic compounds) in response to wounding (Maunoury-Danger et al. 2010). This could explain why wounded (half-girdled and fully-girdled) trees exhibit similar decreases in EM abundance.

Another interesting observation from this study was that *Cenococcum* was found to be the root dominant in terms of frequency (Bergemann and Garbelotto 2006), and, in this study, was the mycelial dominant from roots and soil. Overall dominance by *Cenococcum* on roots is likely a

reflection of its competitive ability for rapid colonization either by numerous sclerotia (Dahlberg et al. 1997) or proliferation via root-to-root contacts. We expected that *Cenococcum* would occupy a high proportion of EM root biomass due to the high frequency observed on tanoak roots (Bergemann and Garbelotto 2006). In this study, we found evidence that the root hyphal abundance of *Cenococcum* varied across seasons and was unaffected by girdling, a result consistent with the girdling experiments of *F. sylvatica* that showed no effect on EM frequency after girdling (Danneman et al. 2009). However, the greater soil hyphal abundance of *Cenococcum* compared to *Tricholoma* was unexpected given their short-emitting hyphae (Agerer 2001). The higher density of root occupation for *Cenococcum* is a

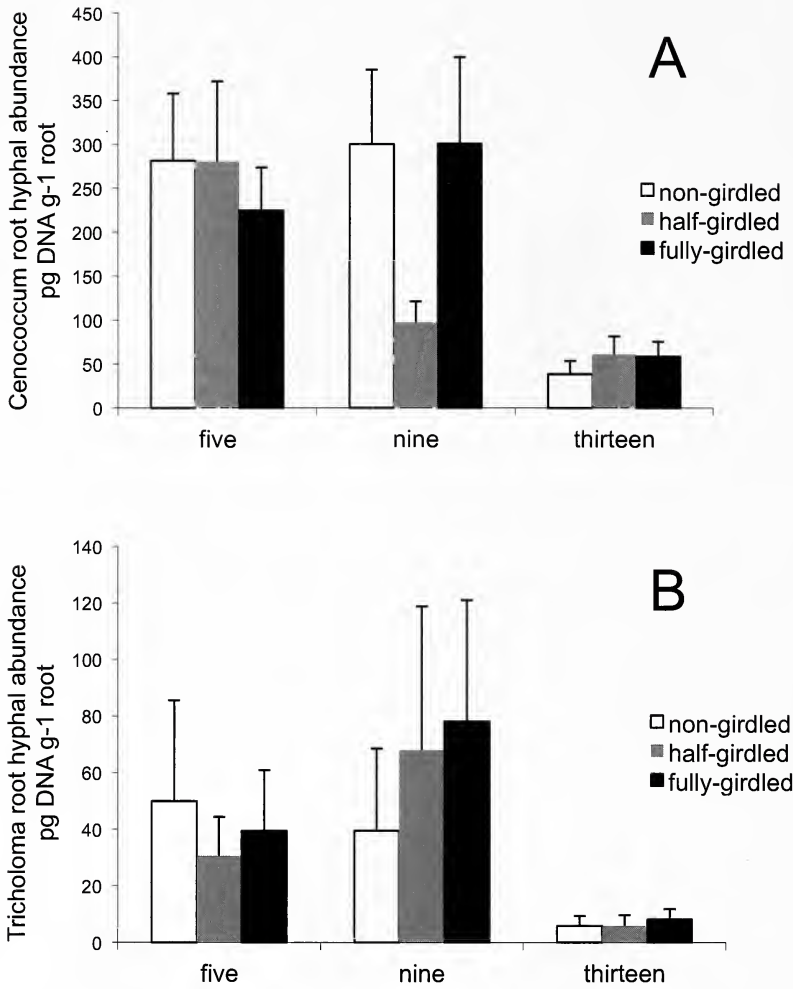


FIG. 3. Root and soil hyphal abundance of *Cenococcum* and *Tricholoma* five (June 2003), nine (October 2003) and thirteen (February 2004) months after girdling *Notholithocarpus densiflorus* trees. Means (+1 SE) are graphed. A. *Cenococcum* root hyphal abundance. B. *Tricholoma* root hyphal abundance. C. *Cenococcum* soil hyphal abundance. D. *Tricholoma* soil hyphal abundance. A significant taxon \times time interaction was observed for ectomycorrhizal root hyphal abundance but not for soil hyphal abundance.

likely explanation for its observed dominance in soil.

Several factors should be taken into consideration when comparing the biomass of taxa and between substrates using qPCR assays. For one, the number of rDNA copies varies considerably between EM species, and the DNA starting quantity inferred from these assays is a function of both the number of copies detected and the template quantity (Landeweert et al. 2003; Raidl et al. 2005). In addition, only a few qPCR studies have found a significant relationship between hyphal abundance and fungal biomass inferred from qPCR (Raidl et al. 2005). Also, a potential error arises from the variation in biomass estimates in different substrates (roots and soil) because of the variation in qPCR kinetics by the various environmental inhibitors in either sub-

strate. Our approach was designed to minimize the inherent variation between substrates by simulating environmental PCR conditions; however, lower hyphal biomass estimates in soil compared to roots may be due to greater PCR inhibition in soil substrates. Despite these limitations, this study demonstrates that this assay affords sensitive quantification of EM genera from mixed-species substrates for comparisons across time and after girdling.

With the observed decline in abundance of the EM extramatrical mycelia, we can only speculate about the possible disruptions to EM function and ecosystem productivity. For example, we expect that plant growth and establishment may be altered with a reduction of EM inoculum (Perry et al. 1989; Nara and Hogetsu 2004), and a decline in EM species richness may accompany

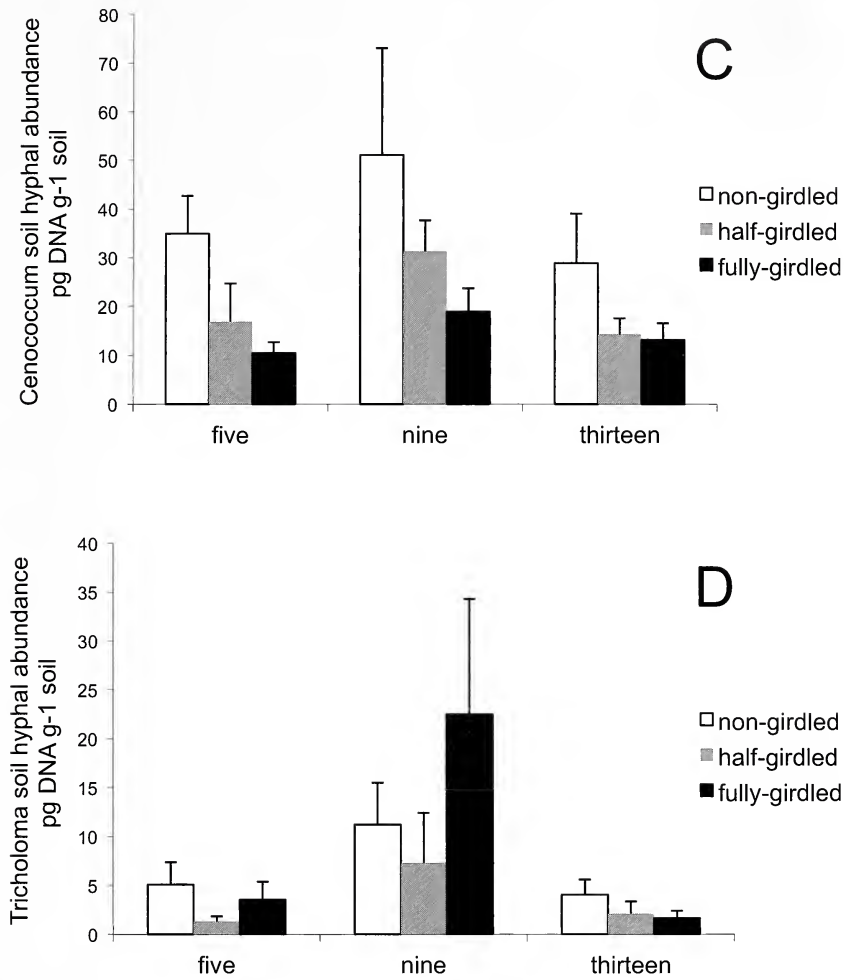


FIG. 3. Continued.

the loss of carbon supply to the roots by girdling (Kaiser et al. 2010; Pena et al. 2010). Also, variation in host-nutrient concentrations after inoculation with EM fungi provides evidence that nutrient acquisition and mobilization is not equivalent among species (Nara 2006), and a decline in carbon assimilate by girdling reduces the activity of EM proteinases that assimilate nutrients from organic matter (Chalot and Brun 1998; Read and Perez-Moreno 2003; Talbot and Treseder 2010). Whether intact mycorrhizal mutualisms in other EM plant species (e.g., Douglas-fir and ericoid plants) will offset the decline in EM richness and function in soils is also unexplored in the present study. From this research, we have gathered evidence that shows a decrease in the extramatrical biomass of EM fungi after girdling; the potential for disruption of ecosystem productivity in stands infected by *P. ramorum* should be considered in future research.

ACKNOWLEDGMENTS

We are grateful for field and laboratory support from several members from the Garbelotto lab including Tami Harnik, Katy Hayden, Rachel Linzer, Lori Miles, Matt Meshriy, Amy Smith, and Steven Swain. The Gordon and Betty Moore Foundation provided funding for this research.

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APPENDIX 1. Taxon, clone identifiers, and GenBank accessions of nuclear ribosomal large subunit sequences from *Notholithocarpus densiflorus* roots to test the specificity of target template DNA and cross-reactivity of non-target template DNA in TaqMan assays.

Fungal taxon	Clone source - GenBank accession	Fungal taxon	Clone source - GenBank accession	Fungal taxon	Clone source - GenBank accession
<i>Alpova</i>	G5 - DQ273499	<i>Cortinarius</i>	Y1 - DQ273507	<i>Piloderma</i>	N3 - DQ273488
<i>Amanita</i>	O16 - DQ273481	<i>Cortinarius</i>	N43 - DQ273508	<i>Ramaria</i>	O4 - DQ273519
<i>Amanita</i>	K11 - DQ273482	<i>Cortinarius</i>	O25 - DQ273509	<i>Russula</i>	Q52 - DQ273528
<i>Amphinema</i>	C13 - DQ273487	<i>Cortinarius</i>	S4 - DQ273510	<i>Russula</i>	K10 - DQ273529
Ascomycota	F22 - DQ273445	<i>Entoloma</i>	D16 - DQ273516	<i>Russula</i>	P50 - DQ273530
Ascomycota	F6 - DQ273446	<i>Galiella</i>	S7 - DQ273473	<i>Russula</i>	Q1 - DQ273531
Basidiomycota	G20 - DQ273490	Gomphaceae	G3 - DQ273518	<i>Russula</i>	N17 - DQ273534
Basidiomycota	D34 - DQ273491	Gomphaceae	C8 - DQ273520	<i>Sebacina</i>	X9 - DQ273535
Basidiomycota	C11 - DQ273492	Gomphaceae	D43 - DQ273521	<i>Sebacina</i>	Y2 - DQ273536
<i>Boletopsis</i>	X33 - DQ273552	<i>Hydnellum</i>	D1 - DQ273539	<i>Sebacina</i>	O17 - DQ273537
<i>Boletus</i>	A34 - DQ273498	<i>Hygrophorus</i>	A61 - DQ273522	<i>Sebacina</i>	N11 - DQ273538
<i>Boletus</i>	F12 - DQ273495	<i>Inocybe</i>	C25 - DQ273513	Sordariomycetes	D11 - DQ273475
<i>Byssocorticium</i>	A1 - DQ273484	<i>Inocybe</i>	A6 - DQ273514	Sordariomycetes	D38 - DQ273477
<i>Byssocorticium</i>	X34 - DQ273485	<i>Inocybe</i>	F59 - DQ273515	Thelephorales	F45 - DQ273548
<i>Cadophora</i>	F13 - DQ273453	<i>Lachnum</i>	D12 - DQ273458	<i>Tomentella</i>	A73 - DQ273540
<i>Cadophora</i>	C34 - DQ273455	<i>Lachnum</i>	F3 - DQ273459	<i>Tomentella</i>	A20 - DQ273541
Cantharellales	P4 - DQ273504	<i>Lactarius</i>	A16 - DQ273524	Thelephorales	A14 - DQ273542
<i>Capronia</i>	C14 - DQ273472	<i>Lactarius</i>	A22 - DQ273525	<i>Tomentella</i>	C70 - DQ273543
<i>Cenococcum</i>	N72 - DQ473308	<i>Macowanites</i>	B11 - DQ273399	<i>Tomentella</i>	A21 - DQ273544
<i>Cenococcum</i>	A27 - DQ273448	<i>Melanogaster</i>	B8 - DQ273497	<i>Tomentella</i>	W54 - DQ273546
<i>Cenococcum</i>	A4 - DQ273450	<i>Mortierella</i>	F58 - none	Thelephorales	D3 - DQ273547
<i>Cenococcum</i>	N72 - DQ473308	<i>Neonectria</i>	D35 - DQ273479	Thelephorales	G1 - DQ273549
<i>Cenococcum</i>	A31 - N/A	Pezizomycotina	A8 - DQ273465	<i>Tomentella</i>	A17 - DQ273551
<i>Cenococcum</i>	B6 - N/A	Pezizomycotina	G60 - DQ273462	<i>Tomentella</i>	F57 - DQ273553
<i>Cenococcum</i>	B19 - N/A	Pezizomycotina	P2 - DQ273464	<i>Tricholoma</i>	G58 - DQ273556
<i>Cenococcum</i>	F20 - N/A	Pezizomycotina	N8 - DQ273466	<i>Tricholoma</i>	R24 - DQ273557
<i>Cenococcum</i>	G14 - N/A	Pezizomycotina	X35 - DQ273467	<i>Tricholoma</i>	F16 - DQ273558
<i>Cenococcum</i>	N69 - N/A	<i>Phialocephala</i>	F11 - DQ273456	<i>Tricholoma</i>	S1 - DQ273559
<i>Cenococcum</i>	T33 - N/A	<i>Phialophora</i>	D44 - DQ273470	<i>Tricholoma</i>	W74 - DQ273560

MORPHOLOGY, PHYSIOLOGY, GENETICS, ENIGMAS, AND STATUS OF AN EXTREMELY RARE TREE: MUTANT TANOAK

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ABSTRACT

Important physical characteristics, morphological attributes, physiological functions, and genetic properties of mutant tanoak, *Notholithocarpus densiflorus* f. *attenuato-dentatus* (Fagaceae), and normal tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh, were studied on the Challenge Experimental Forest in Yuba Co., California in an attempt to explain the cause of the mutation and to determine where in the tree it was manifest. Leaves, stomata, trichomes, foliar nutrients, photosynthesis, transpiration, internal moisture stress, DNA, and genetics (metabolomics) all were examined in detail. In some instances, the plant part or the process favored the mutant; in others, the normal tanoak exceeded. Susceptibility to *Phytophthora ramorum*, the sudden oak death pathogen (SOD) was similar. No all-encompassing functional difference for either type was indicated, other than the size and shape of the leaves and the metabolites in them. We know the two tanoak types differ genetically, but more complete genomic analysis is needed to pinpoint the cause of the mutation. Some thought-provoking enigmas concerning the morphology and physiology of tanoak are presented along with the status (number of plants and location) of the rare mutant.

Key Words: DNA, ecology, genetics, mutant and normal tanoak, *Lithocarpus densiflorus*, *Notholithocarpus densiflorus*, physiology, status.

The mutant form of tanoak, *Notholithocarpus densiflorus* f. *attenuato-dentatus* (Fagaceae) (Tucker et al. 1969) (Fig. 1), is extremely rare in a natural setting. Knowledge of this mutant, the cause of its condition, and its future as a tanoak derivative not only could add to our understanding of the genus *Notholithocarpus*, but also might have practical value by giving a clue for lessening the impact of sudden oak death (SOD).

Tanoak is an evergreen hardwood that is considered a link between the chestnut (*Castanea*) and the oak (*Quercus*) (Sudworth 1967). It has flowers like the chestnut and acorns like the oak. Over the years, taxonomists have had difficulty classifying the species. According to the synonymy in Little (1979), tanoak was listed as *Quercus densiflora* in 1840, *Pasania densiflora* in 1867, and *Lithocarpus densiflorus* in 1916. Recently, another genus classification has been established (*Notholithocarpus*; Manos et al. 2008) that separates the single North American tanoak from the far-eastern genus *Lithocarpus*.

Tanoak is a medium-sized tree that grows best on the moist, west-facing slopes of the Cascade Range and Sierra Nevada in Oregon and

California southward to Santa Barbara Co. It usually occurs in a complex mixture with conifers and other hardwoods or in pure, even-aged stands (Tappeiner et al. 1990). Tanoak forms single trees or clumps of two to five trees that originate from root-crown sprouts.

Tanoak is a member of a large group of plants called “broad sclerophylls,” which are considered to be well adapted to a wide variety of environments (Mooney and Dunn 1970; McDonald 1982). At least part of the evidence for this classification is found in the fossil record—paleobotanists have traced this species back 12–26 million years to a period during the late Oligocene to mid-Miocene epochs (Cooper 1922). Tanoak has survived volcanism, glaciation, upheaval, and subsidence in at least part of its present range. Consequently, adaptation to heat, cold, and drought are likely to be part of tanoak’s genetic makeup. Having existed for millions of years, tanoak is considered to be an evolutionary species or lineage—“It is a lineage, an ancestral-descendant sequence of populations existing in space and in time.” (Grant 1971, p. 38).

Tree seedlings with peculiar leaves and a low, shrubby form (Fig. 1) were first discovered on the



FIG. 1. At about 2 m in height, this was the largest mutant tanoak on the Challenge Experimental Forest, Yuba Co., California in August 1967. It disappeared shortly after this photo was taken. (Photo credit: Tucker et al. 1969).

USDA Forest Service's Challenge Experimental Forest (maintained by the Pacific Southwest Research Station, Albany, CA) in Yuba Co., California in January 1962. Believed to be some form of mutant, the identity of these trees was not immediately apparent.

Their location, however, gave a clue to their origin. About 20 mutant seedlings were found scattered beneath a large, open-growing tanoak "mother tree" along with scores of normal seedlings. To prove tanoak parentage, acorns were gathered beneath this and nearby trees in the fall of 1965 and germinated in pots in a greenhouse. Of the 45 acorns that germinated, one clearly was a mutant (Tucker et al. 1969).

Why were the mutants so weak and slow growing? What was causing their formation? What were the odds that all of them would die and be lost to botanists and other interested disciplines, possibly forever?

A chromosomal aberration was suspected, and squash preparations to examine chromosome counts were carried out on several occasions. All attempts were unsuccessful (Tucker et al. 1969). A

likely hypothesis was advanced by Robert Echols, a Pacific Southwest Research Station geneticist, who suggested that the aberration, a sublethal recessive condition, could have been caused by selfing (self-pollination).

By 1969, 10 tanoak mother trees with mutant seedlings nearby were located on or near the Experimental Forest. These trees were quite similar with fully developed, wide-spreading crowns and a shaded, deep organic layer beneath them. Almost all mutant seedlings were 3–40-cm tall and appeared to be in poor health with little or no growth.

In 1974, a mother tree with both mutant and normal seedlings beneath was visited again, and not a single mutant could be found. The spring of 1973 was particularly cold, and the abnormal temperatures could have been lethal to the mutants, but not to the normal seedlings. Over the years, all of the known mother trees at Challenge died, were inadvertently lost to wood cutters, or could not be relocated.

As interest increased, the search for mutant tanoaks accelerated, and seedlings beneath hundreds of tanoaks were examined both on the Experimental Forest and throughout most of the species' natural range. Botanists and silviculturists on many national forests were questioned, and a herbarium specimen was shown to several, but no additional mutants were found.

The objective of this paper is to report our findings on the physical characteristics, morphological attributes, physiological functions, and genetic properties of the mutant tanoak in an attempt to characterize the mutation, learn where it manifests, and understand its population dynamics. Another objective was to look for something (anything) in the mutant that might help curtail the ravages of SOD. To help achieve these objectives, we compared the mutant to a normal tanoak of about the same age and development growing nearby. Any differences that we found could then help to isolate critical elements in the mutant, and possibly lead to a genetic explanation of its mutancy.

METHODS

The study was located on the Challenge Experimental Forest in north-central California (Yuba Co.), T19N R7E, MDM sect. 20. The forest cover type in the vicinity of the study site is Pacific ponderosa pine–Douglas-fir (SAF type 244) (McDonald 1980). Several conifer and hardwood species characterize this type, and species near the sample trees included ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson. var. *ponderosa*), Pacific madrone (*Arbutus menziesii* Pursh), and many tanoak seedlings, saplings, and trees. (Scientific and common names of



FIG. 2. Mutant tanoak tree sampled in this study on the Challenge Experimental Forest, Yuba Co., California.

trees are from Little [1979].) In terms of ecological subregions of California, the area corresponds to section M261E Sierra Nevada and the granitic and metamorphic hills subsection (Miles and Goudey 1997).

The original forest was logged (at least for the largest and best conifer trees) from about 1860–1890 (McDonald and Lahore 1984). Thus, logging and the inevitable fires caused the current forest to be a mosaic of even-age, second-growth stands. Summers on the Experimental Forest are hot and dry; the winters cool and moist. The mean annual temperature is 16°C. The growing season is about 200 days. Average annual precipitation is 1720 mm with 94% falling between October and May (USDA Forest Service unpublished). A typical soil series (Aiken) grades from loam to clay-loam with depth, and is deep, moderately well drained, and quite fertile.

By 2009, no mutant seedlings at Challenge could be located anywhere, and only three larger entities remained. These consisted of a slender moribund tree with a 50° lean, a clump of root-crown sprouts, and a single upright tree.

The best chance for achieving the objectives was to sample the most representative of the mutants. The severely leaning moribund specimen was not suitable, and the root-crown sprouts had severe limitations. Of the seven

root-crown sprouts, five were alive, although one was top-dead with only two living lower branches. The remaining four trees had breast-height diameters that ranged from 2.2–7.5 cm and heights from 5–11 m. The age of the tallest root-crown sprout was 22 yrs at breast height and 26 yrs at 30 cm above mean ground line. All were leaning 20–40° away from a large pine 1.5 m to the north. Another negative was that no similar-sized, normal tanoaks were nearby.

Plainly, the single upright mutant tree was from seed and not a root-crown sprout. It and several similar-sized, normal tanoaks were located at the 825 m elevation on level ground. One normal tanoak was randomly chosen. Both the mutant and normal sample trees lean about 20° into a small opening, and although shorter than surrounding trees, are not overtopped.

Sampling of the mutant tree began on August 14, 2008, when basic data on it and the normal tanoak tree nearby were taken (Fig. 2). Both trees were bored with a standard increment borer at two places on the stem, and the rings counted to determine age.

Leaves from the mutant and the normal tanoak were gathered from small branches cut at mid-crown with a long-handled pruning pole. Sampling time was from 1000 to 1400 hrs PST. A sample of leaves was gathered from more than 30

normal tanoak trees in the surrounding area for DNA analysis. Additional leaves were gathered for other tests as needed.

To determine stomatal density and aperture length, three leaves from both the normal and mutant tanoaks were randomly selected. Stomatal density was determined for both the upper and lower leaf surfaces using imprints made with transparent nail varnish. The number of stomata per mm² was then recorded in three randomly selected areas and measured under a stereomicroscope equipped with an ocular micrometer. Stomatal aperture lengths, defined as the distance between the junctions or ends of the guard cells, were also measured on ten stomata from each leaf type. Only stomata from the lower or underside of the leaves were used for this measurement.

We were also interested in the trichomes on the underside of the leaves. Trichomes are a beneficial adaptation for the species because their fuzzy nature is both anathema to hungry herbivores (King and Radosevich 1980), as well as an effective means for reducing transpiration. Sampling was accomplished by pressing a small piece of electrical tape to the midrib and the leaf blade, and then sticking the tape to a standard microscope slide. Sampling intensity was 10 leaves from each tanoak type. Trichomes were counted along two transects on the midrib and two plots on the blade with a dissecting scope. Each transect was a long rectangle with an area of 2.8 mm², and the blade plots were 16.3 mm² in size.

Foliar analysis followed standard protocols (Bremner 1970) with drying, grinding, and digesting with acid (Kjeldahl) to determine the percentages of each macronutrient (nitrogen, phosphorus, potassium), and a mass spectrometer to indicate parts per million of the micronutrients and metals (aluminum, boron, calcium, copper, iron, magnesium, sodium, sulfur, sodium, and zinc) in the tanoak leaves.

Photosynthetic gas exchange was measured on August 14 for both the mutant and normal tanoak leaves with a Li-Cor 6400 portable photosynthesis system with a red/blue LED light source and CO₂ injector (Li-Cor Inc. Lincoln, NE), by setting photosynthetically active radiation (PAR) from 1500 to 1000, 500, 200, 100, 50, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. We let the leaves acclimate in the cuvette for three minutes before each measurement. The temperature within the cuvette was maintained near the ambient air temperature (31°C). A constant CO₂ concentration at 380 $\mu\text{mol mol}^{-1}$ was supplied with fixed air flow of 500 mol s^{-1} . Data were taken from two healthy leaves on each tree. We fit these data with the non-rectangular hyperbolic model developed by Hanson et al. (1987).

During the measurement of gas exchange, internal water potential was measured with a

pressure chamber (PMS Instrument Company, Corvallis, OR) on small twigs with leaves attached at each sampling time. In addition, we measured average soil moisture content from the soil surface to the 20 cm depth with a CS 620 Water Content Hydrosense (Campbell Scientific, Inc., Logan, UT) at four locations around both the mutant and normal trees. It was 7.9% with a standard deviation of 1.7% by volume.

The first approach we took to understand the genetic differences between the mutant and normal tanoaks was a relatively new technique called metabolomics (Macel et al. 2010). It involves identifying the metabolites found in the leaf tissue of both the mutant and normal tanoaks. If the mutation impacts a metabolic pathway, differences between the two forms of tanoak can be determined, and these could suggest what gene(s) are involved in the mutation. Sampling intensity was six leaves from the mutant and two leaves each from three normal trees. Additional normal trees were included in this part of the study, as we wanted to sample the range of metabolites that were present in surrounding trees. Leaves were stored on dry ice until transported to the UC Davis Metabolomics Core Facility where they were prepared and analyzed using standard protocols. Based on mass spectrometry, peaks for a range of metabolic products were produced and analyzed using principal components analysis (PCA). This technique is ideal for summarizing multivariate data.

The second genetic approach we took was to examine variation at putatively neutral microsatellite loci. DNA was extracted from the leaves of the mutant tanoak and from those of many normal trees nearby and analyzed in the laboratory of Richard Dodd at UC Berkeley. Extraction protocols as well as chloroplast and nuclear DNA marker analyses followed Nettle et al. (2009). Five polymorphic chloroplast markers and 11 nuclear microsatellite markers were scored.

In the mid-1990s a new disease affecting tanoak surfaced on the West Coast of California and spread rapidly to several counties in coastal California and Oregon. It is called sudden oak death (SOD) and is caused by a fungus-like microorganism named *Phytophthora ramorum*. In some infected trees, cankers appear, the bark splits, the wound oozes, and as early as 6–24 mos after infection, the tree dies. Thus far, the disease has not spread to wildlands in drier locales east of the Cascade Range and the Sierra Nevada.

To determine if the mutant tanoak was more or less susceptible than normal tanoaks to SOD, leaves from the mutant and nearby normal tanoak trees were inoculated with the pathogen and tested for susceptibility using a detached leaf assay (Hayden et al. 2011). This work was performed in the laboratory of Matteo Garbelotto at the University of California, Berkeley.

RESULTS AND DISCUSSION

Physical Characteristics

Branch angle, bark roughness, and bark color were similar for the two sampled trees. Diameter at breast height (1.4 m), diameter at 30 cm above mean ground line, and tree height were quite similar as well (Table 1). Both sample trees grew slowly when young and then faster after reaching breast height. Each eventually produced flowers, but no acorns.

The unique physical characteristics and morphological attributes of the two types of tanoak leaves and their stomata and trichomes have an important physiological role. Leaves from the normal tanoak were shorter and wider and had three times as many stomata as those from the mutant, but the number of trichomes was significantly fewer. In general, more open stomata mean more carbon dioxide intake, and a higher potential for increased transpiration, but the higher trichome density on mutant leaves could elevate the boundary layer and lower the ability of the wind to “pull” moisture from them.

Morphological Attributes

Leaves of the two forms of tanoak constituted the place where the most obvious differences became manifest (Fig. 3). Leaves from the mutant tree were 20% longer and 57% narrower than leaves from the normal tanoak tree (Table 2). Both dimensions differed statistically ($P < 0.05$), with the differences directly translated into significantly smaller leaf areas and lower, but not significantly lower, dry weights of the leaves from the mutant tree. The width of the mutant leaves was narrow regardless of length, but the width of the leaves from the normal tanoak tree increased in proportion to length.

The distinct difference in leaf shape suggests a possible biophysical advantage for the mutant type in leaf level temperature and thus transpirational water loss. We used a simplified energy balanced equation where incident radiation, emissivity, absorption, and transpiration rate ($4 \text{ mmol m}^{-2} \text{ s}^{-1}$) were considered equivalent for leaves from both trees (Nobel 2005). At ambient temperatures above 30°C and low wind speeds (1 m s^{-1}), leaf temperature of the mutant

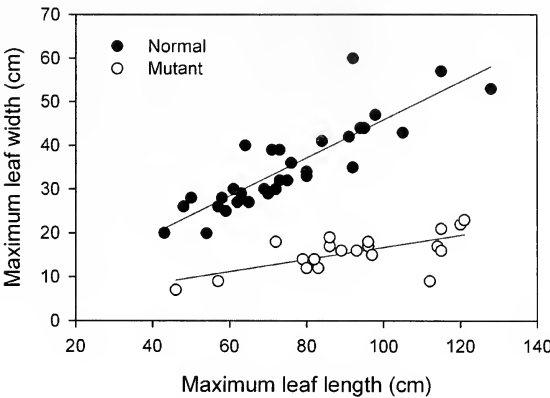


FIG. 3. Relationship between width and length of mutant and normal tanoak leaves collected from individual trees near the Challenge Experimental Forest, Yuba Co., California.

tanoak was nearly 2°C less than leaves of the normal tree.

For leaves from both trees, only a few stomata were observed on the upper side of the leaves and many more on the lower side. For the upper side, a standard t-test indicated no statistically significant difference in stomatal density between the two tanoak types, but for the lower side, three times as many stomata on the average normal leaf were present versus that of the mutant—a highly significant difference (Table 3). No statistical difference between the two tanoak types was found for aperture length with the overall average being $25.0 \pm 2.5 \text{ }\mu\text{m}$.

The “center and arms” configuration of the tanoak trichomes, their curving, twisting shape, and their high density indicate an underside leaf surface that could influence internal water relations of the two tree types (Fig. 4). A standard two-tailed statistical test showed significant differences between the mutant and the normal trees. Leaves from the mutant tree had significantly more trichomes on both the midrib ($P < 0.0001$) and the blade ($P < 0.0002$) than did the normal leaves (Fig. 5).

Foliar analysis indicated no statistically significant differences between the two tanoak trees in the percentage of nitrogen, phosphorus, or potassium (Table 4), but did show significant differences ($P < 0.05$) in several micronutrient elements (boron, calcium, copper, manganese, and zinc). Nearly all elements in the mutant were substantially less than in the normal tree. Although there were no differences in the elemental concentration of nitrogen, the concentration per unit area was 60% greater in leaves from the mutant tree than in the normal leaves (0.08 versus $0.05 \text{ mg kg}^{-1} \text{ cm}^{-2}$).

The lower internal leaf temperature of the mutant would decrease the leaf-air water vapor concentration gradient, lower transpirational

TABLE 1. PHYSICAL CHARACTERISTICS OF MUTANT AND NORMAL TANOAK TREES. Challenge Experimental Forest, Yuba Co., California.

Tree	Age at breast height (years)	Age at 30 cm (years)	Height (m)	Diameter (cm)
Mutant	22	26	10.9	9.0
Normal	20	28	11.8	11.4

TABLE 2. MEAN MORPHOLOGICAL CHARACTERISTICS (AND STANDARD DEVIATION) OF LEAVES FROM NORMAL AND MUTANT TANOAK TREES. Challenge Experimental Forest, Yuba Co., California. *Indicates a significant difference (t-test, $P < 0.05$).

Tree	Number	Length* (mm)	Width* (mm)	Area* (cm ²)	Dry weight (g)	DW/area* (g cm ⁻²)
Normal	32	75.5 (19.7)	35.2 (11.2)	21.9 (11.2)	0.23 (0.13)	0.010 (0.001)
Mutant	20	92.0 (20.4)	15.6 (4.3)	13.6 (5.4)	0.18 (0.07)	0.013 (0.001)

TABLE 3. COMPARISON OF STOMATAL DENSITIES (PER MM²) FOR LEAVES FROM A NORMAL AND MUTANT TANOAK TREE. Challenge Experimental Forest, Yuba Co., California.

Leaf side	Number	Normal	Mutant	t-test	P
Upper	9	4.6 ± 2.0	2.8 ± 2.0	-0.65	0.52
Lower	9	358.6 ± 28.0	105.5 ± 40.0	-4.64	0.0003

water loss, and possibly maintain a more favorable leaf-water status for continued carbon assimilation. This would become particularly important during the hot, dry summers typical

of the Sierra Nevada in the Challenge Experimental Forest area, but less so in the deep-shade environment of the sample trees. Leaf-level carbon assimilation is also dependent on nutrient status, and the lack of statistical differences between the two tanoak types for nitrogen, phosphorous, and potassium indicates no advantage for either type. The effects of significantly lower amounts of some of the minor elements and heavier metals in the mutant tanoak are unknown.

Physiological Functions

We found that maximum net photosynthesis (maximum assimilation rate, A_{max}) differed substantially between the mutant and normal tanoak trees (Fig. 6). A_{max} was $2.51 \mu\text{mol m}^{-2} \text{s}^{-1}$ for leaves from the mutant tree and $1.19 \mu\text{mol m}^{-2} \text{s}^{-1}$ for those of the normal tanoak. The light compensation point and dark respiration were $12.84 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $-0.34 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, for leaves from the mutant tree and $15.63 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $-0.22 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, for leaves of the normal tanoak. Quantum yield (the efficiency with which incoming

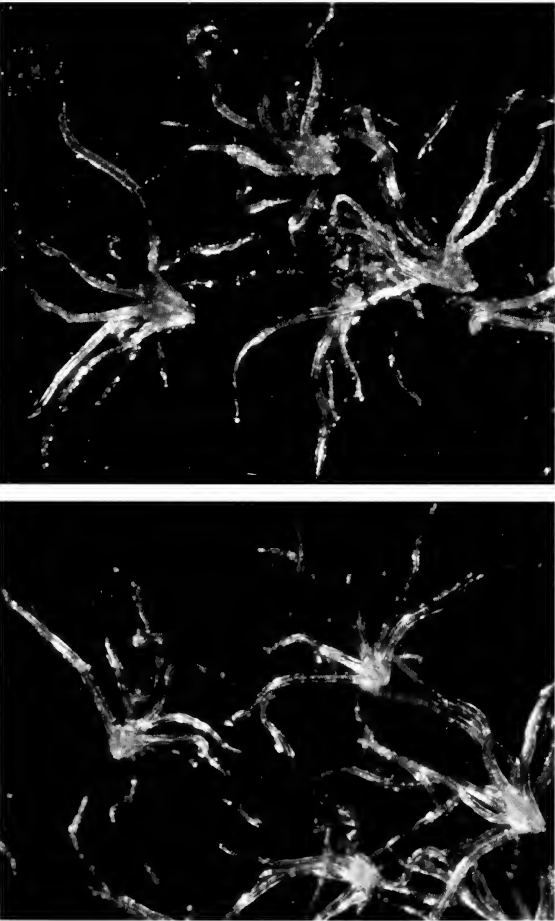


FIG. 4. Microphotograph of trichomes on mutant tanoak leaves (upper) and normal leaves (lower). It is interesting that the mutant condition greatly affected the size and shape of the leaves, but not the size and shape of the trichomes.

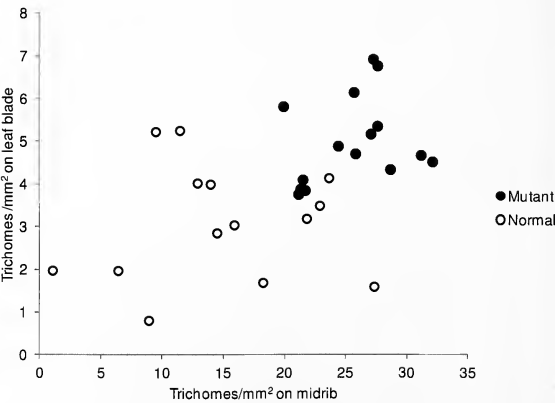


FIG. 5. Relationship of trichomes on blade and midrib of mutant and normal tanoak leaves.

TABLE 4. MEAN NUTRIENT CONTENT (AND STANDARD DEVIATION) OF LEAVES FROM A MUTANT AND NORMAL TANOAK TREE. Challenge Experimental Forest, Yuba Co., California.

Nutrient	Mutant	Normal
N (%)	1.10 (0.16)	1.14 (0.04)
P (%)	0.05 (0.001)	0.05 (0.002)
K (%)	0.48 (0.02)	0.43 (0.03)
Ca (%)	0.78 (0.03)	1.00 (0.11)
Mg (%)	0.14 (0.01)	0.15 (0.01)
S (%)	0.09 (0.01)	0.10 (0.01)
Al (ppm)	98.0 (18.7)	151.0 (60.7)
B (ppm)	25.2 (0.8)	45.8 (5.9)
Cu (ppm)	5.3 (0.56)	19.3 (14.5)
Fe (ppm)	119.0 (21.0)	164.0 (52.0)
Mn (ppm)	1124.0 (33.0)	2685.0 (157.0)
Na (ppm)	13.9 (1.2)	19.9 (6.6)
Zn (ppm)	14.4 (0.6)	26.6 (6.4)

light is converted to carbohydrates within a leaf) was higher in mutant leaves (0.028 mol CO_2) (mol incident photon) $^{-1}$ than in the leaves of the normal tanoak (0.015 mol CO_2) (mol incident photon) $^{-1}$.

Internal water potential was much more negative in the mutant tree than in the normal tree from 11:00–13:00 PST (Fig. 7). Both tanoak trees recovered at 14:00 PST. Considering a higher A_{max} in the mutant than in the normal tanoak, this suggests that the mutant tanoak is more tolerant of internal water stress than the normal tanoak.

Higher A_{max} and quantum yield, and a lower light compensation point in the mutant tanoak than in the normal type, indicates that the mutant tanoak is more efficient not only in capturing light from sun flecks under the tree canopy, but also at high PAR (photosynthetically active radiation) for carbon gain (Fig. 6). Furthermore, the mutant showed more negative leaf-water

potential than in the normal type (Fig. 7), which suggests a higher tolerance for water stress in the mutant.

Genetic Properties

Metabolomics. More than 220 individual metabolites were profiled using mass spectrometry metabolomic analyses. Of these, 41 were identified and the rest were unidentified peaks. Each peak is the result of the mass spectrometer detecting a different potentially unidentified metabolite. Because of the large number of metabolites, a multivariate approach, and particularly a principal component analysis (PCA) was used. Each PC explains a certain percent of the variation in the metabolite data. PC1 explained 26% of the variation in the data, while PC2 explained 18% (Fig. 8). The analysis showed substantial differences between the single mutant and the three normal trees, particularly along the second principal component (PC2). Metabolites that loaded positively onto PC2 included myo-inositol, xylonic acid, gluconic acid, phosphoric acid,

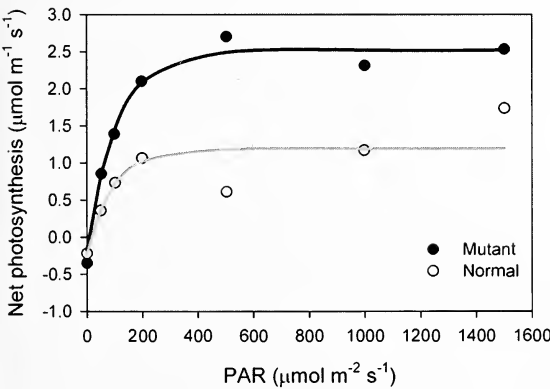


FIG. 6. Net photosynthesis ($n = 2$) at different photosynthetically active radiation levels for two leaves on mutant and normal tanoak trees on the Challenge Experimental Forest, Yuba Co., California. Lines are modeled with Hanson et al. (1987)'s equation. The relationship between measured and modeled values was $r^2 = 0.98$, $P < 0.001$ for the mutant leaves and 0.73 , $P < 0.05$ for the normal leaves.

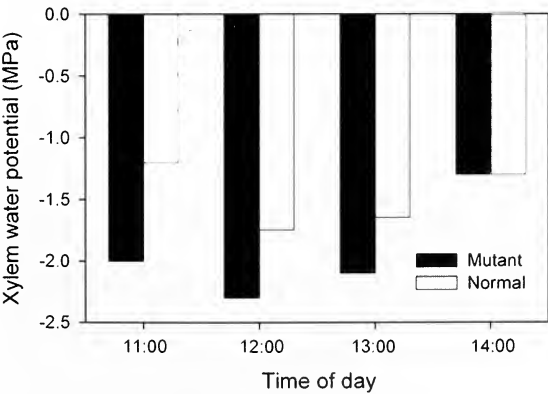


FIG. 7. Water potential of leaves on small twigs from mutant and normal tanoak trees at four sampling times, Challenge Experimental Forest, Yuba Co., California.

lactobionic acid, ribitol, serine, and isoleucine, along with a number that were unidentified.

Most classical genetic studies depend on the ability to create crosses, and in this instance crosses would be the most efficient means of understanding the genetics underlying the mutation. Since the mutants do not produce acorns, this technique is not possible; however, other tools are available that do not rely on crosses. The relatively new technique of metabolomics identified the metabolites in the tissue of each tanoak type. Analysis of the leaves of the two tanoak types showed very different metabolic profiles, even with similar tissue being collected in close proximity at the same time. Because metabolites are the product of proteins and enzymes that in turn are produced by RNA (and thus DNA sequences), these different metabolic profiles suggest that genetic differences exist between the two tanoak types. Because of the fluid nature of metabolic pathways, it is difficult to predict exactly which genes contain the genetic differences. The next step would be more genetic research, and particularly an analysis of the transcriptome (all of the mRNA or expressed genes in the tissue). This would help identify the genes that were associated with the changes in metabolites observed in this study.

Microsatellite variation. Based on the foliar sample from the 30 tanoak trees in the surrounding area, their DNA tells us that the mutant tanoak tree is similar to other local tanoaks and thus truly is a mutant in its genome, and not a hybrid or some other aberration. Both the mutant tree and normal forms were haplotype E, typical for tanoak trees elsewhere in the Sierra Nevada (Nettel et al. 2009). Nuclear microsatellite alleles did not differ between the mutant and the normal trees in the surrounding forest.

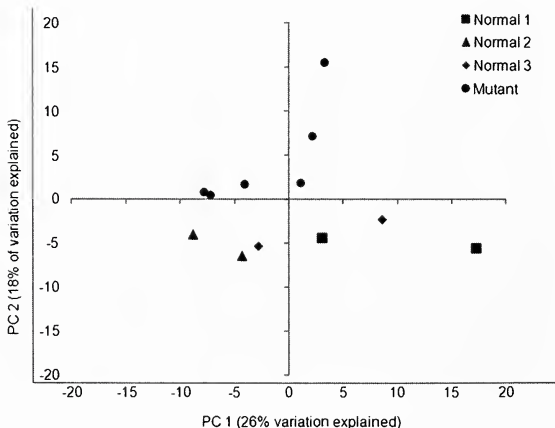


FIG. 8. Principal component analysis of metabolomic data based on two leaves from three normal tanoak trees and six leaves from the mutant tree.

Results of the nuclear and chloroplast markers indicate that the mutant is not a hybrid and that it originated in the local population. If there had been some hybridization or long-distance gene flow, we would expect to see a different genotype at the chloroplast loci. Instead, the mutant was observed to be the local haplotype. Also, because only a small number of microsatellite markers were used for our analysis of putatively neutral genetic variation, it is unlikely that our markers would be at or near the genetic mutation. In the future, a more complete genomic analysis may allow the specific mutation to be identified.

This result lends support to the theory that a mutation occurred in one or more genes that produced the unique phenotype. The most likely scenario is that the mutation occurs at a low frequency across the population. The mutant phenotype appears only in homozygous individuals, and heterozygous trees are fully fertile. Homozygous mutant offspring are continuously produced, but because of their metabolic differences, are unable to germinate and/or to produce seedlings except on rare occasions. And even when seedlings are produced, they tend to be weak and short-lived.

In 1994, mutant tanoak seedlings were found at two widely separated locations on the Klamath National Forest. Nine plants were found at the first location and 16 at the other. All were seedlings 2–45 cm tall. In 2009, none could be found. This supports the idea of a recessive, near-lethal gene or genes that are being preserved in the population. It might even suggest heterosis—the higher fitness of heterozygous individuals that preserve the allele at a higher frequency than might be expected.

Relative to SOD, post-inoculation lesion growth was similar in the mutant and normal tanoak leaves; hence there was no indication of a difference in susceptibility to SOD. However, research on SOD is continuing and is both intensive and extensive. A continuing effort seeks to find tanoak trees with natural resistance, but none have been found to date (Hayden et al. 2011).

A possible avenue of research on SOD involves the leaf trichomes. The inoculation technique that was used involved introduction of the inoculum through a cut in the leaf petiole. Suppose the inoculum was applied over the leaf and hence above the trichomes. This begs the question if so doing prevents spores from actually reaching the leaf surface, which would be beneficial, or would the trichomes hold water closer to the leaf surface, which would be a negative because it would aid penetration through the leaf tissue.

Enigmas

Grant (1971) noted that an evolutionary species has “its evolutionary tendencies, being

susceptible to change in evolutionary role during the course of its history.” Perhaps, “evolutionary tendencies” suggests that the species evolves into many forms and functions as it copes with an ever-changing environment during the millions of years of its existence on the planet. It might even be possible that the mutant will someday become well-adapted and reproduce. Enigmas could well be part of the evolutionary process.

Adaptation to drought is a major characteristic of the broad sclerophylls, and tanoak has many morphological and physiological structures and functions that promote this adaptation (McDonald 1982). However, its current natural range is characterized by a cool, moist climate with high levels of rainfall, fog, or relative humidity, not an environment that would seem to favor adaptation to drought.

Other enigmas concern the shrub form of tanoak as well as an instance of curious demise. The recognized shrub form, *N. densiflorus* var. *echinoides* (R. Br.) Manos, Cannon & S. H. Oh, in the mountains of northern California and southern Oregon is erect and has small leaves. It occurs “on high mountains” (Sudworth 1967), “on dry slopes from 610 to 2440 m” (Munz and Keck 1959), and between 600–2000 m (Tucker 2012). It is also found on much better and moister sites in the northern Sierra Nevada at the 1370–1525 m elevation, where it produces robust clumps of stems after cutting or burning (McDonald and Litton 1993). These grow upright for a few years, lean over, and then straggle downslope for 5 m or more. Here, the leaves are much larger than those of counterparts on poor sites, and are as large or larger than those of the tree form at the 760–1065 m elevation.

The curious demise took place on the Challenge Experimental Forest in an area having many normal and unusual clumps of tanoak sprouts from parent-tree root crowns. All clumps showed two or three generations of sprouting. Here, McDonald et al. (1988) sampled 19 clumps characterized by chlorotic leaf color, an abnormally large number of sprouts, a vastly different height-width relationship than healthy sprout clumps nearby, and a peculiar flat top with no tendency toward dominance by any sprout. After much testing, no pathogens or viruses that could account for the abnormal development were found in field or laboratory, and the reason for the decline and eventual death of the clumps was unknown.

On a much smaller scale, some morphological and physiological adaptations of tanoaks are enigmatic. For example, tanoak stomata are buried in crypts below the leaf surface and as noted earlier, have thousands of trichomes above. Both serve to reduce transpiration, and one would expect seedlings to be drought tolerant. However, research on six-year-old tanoak seed-

lings planted into a common garden on the Challenge Experimental Forest has shown a curious pattern of internal moisture stress during the summer. The seedlings were planted into an open field, under full sunlight. At the first hint of light in the morning, most stomata open most of the way (McDonald and Tappeiner 2002). This rapidly increases transpiration to the point that the loss in internal moisture exceeds the seedling’s daylight recharge capability—leading to eventual death. Efficient recharge ability at night only prolonged the process in these exposed seedlings. It appears that the inability to control the timing and degree of stomata opening trumps the morphological adaptations.

The timing, size, and condition of tanoak seed crops represent additional enigmas. It is likely that very few seed crops produce mutants, and we have no idea when the next will occur. Several complex transactions such as the interplay of high and low temperatures in the spring, selfing, ovule abortion, and others, could be a part of the process of mutant formation.

Seed crops of tanoak were quantified each year on the Challenge Experimental Forest from 1958–1981 (McDonald 1992). Seed was produced in 13 of the 24 yrs of record and amounted to three crops rated as very light, six as light, two as moderate, and two as heavy. A very light seed crop was recorded in 1958, and it is possible that the first mutant seedlings found in 1962 could have come from that crop.

We do know that mutants existed for at least four years beneath one mother tree and all were gone five years later. Anecdotal evidence suggests that not more than 50 mutant tanoak seedlings at least one year old were found at Challenge from 1962–2009.

Status

Because the mutant was so rare and its existence so precarious, cuttings from a short shrub at Challenge were sent to various arboreta and public gardens in California and Washington as insurance for its continued existence (W. Sundahl, USDA-Forest Service, Pacific Southwest Research Station, personal communication). Of those sent, many died or all records of them were lost. The most successful propagation was conducted by Arthur and Maren Kruckeberg at the MsF Rare Plant Nursery (now Kruckeberg Botanic Garden) near Shoreline, Washington. These cuttings were rooted with difficulty, and grown into small bushes or trees. Cuttings were then taken from them, rooted, and sold far and wide over the years (A. Kruckeberg, Univ. of Washington, personal communication). Two trees from the original propagation are now about 15 m tall and 12 m wide, and reside in the Botanic Garden. Healthy mutant tanoak trees

have been reported from several locations in western Washington, Oregon, and California, as well as Great Britain and the Netherlands. All successful propagations reside in well-tended, park-like settings having rich, fertile soil with plentiful water and shade. A few other nurseries also root cuttings and sell them, but none had specimens for sale in their 2009 catalogs. Of importance is that all the mutant tanoaks that are known originally came from the Challenge Experimental Forest.

We have shown that the mutant tanoak seems to be as well adapted to the narrow environment of deep shade and fertile soil as its normal counterpart nearby. However, evidence suggests that mutant tanoak seedlings cannot begin life and grow well in a less benign environment. Even in tended gardens, the cuttings must have shade, deep soil, and possibly fertilizer when young.

The odds of this mutant ever becoming a viable species are low. If the mutant could get past the initial sterility and inviability bottlenecks, it would have difficulty becoming established in a thriving population of non-mutant individuals (Grant 1971).

Daubenmire (1959) noted "Of the thousands of genes that govern the behavior of an organism, only one needs to change beyond a certain extent in order to disturb the synchrony of the various functions and thereby prove fatal. The vast majority of genetic variations are probably unsuccessful because the physiologic balance has been upset by the new combination of genes. Thus there is an internal requirement for harmony in addition to the demand for harmony between the new gene complex and the environment."

As noted earlier, tanoak is regarded as an evolutionary species, meaning as Grant (1971) suggests that it occupies an ecological niche of its own in nature for which it is especially adapted.

TAXONOMIC TREATMENT

Notholithocarpus densiflorus (Hook. & Arn.) Manos, Cannon & S. H. Oh f. **attenuato-dentatus** (J. M. Tucker, Sundahl, & D. O. Hall) McDonald, Zhang, Senock & Wright comb. nov. Fig. 1. Basionym: *Lithocarpus densiflorus* (Hook. & Arn.) Rehder f. *attenuato-dentatus* J. M. Tucker, Sundahl, & D. O. Hall, Madroño 20:224–225. 1969.

CONCLUSIONS

Both normal tanoak and its mutant present many enigmas. We have endeavored to study and express some of the physical, morphological, physiological, and genetic attributes of both types of tanoak. We have noted several enigmas in the

normal tanoak, which potentially suggest that it has changed both morphologically and physiologically during its millions of years of existence on the planet. These changes are likely a response to an ever-changing climate. Our efforts have been both extensive and intensive, and we have gained in knowledge. To paraphrase a noted novelist: "Knowledge is like a river; the deeper it is, the less noise it makes." Perhaps, a bit more noise in the form of more research, especially in genetics, is needed. In that sense, our work here is a base from which that work can proceed.

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THE PAST, PRESENT, AND FUTURE OF *NOTHOLITHOCARPUS DENSIFLORUS* (TANOAK) AS A FOREST PRODUCTS RESOURCE

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ABSTRACT

Notholithocarpus densiflorus (Hook. & Arn.) Manos, Cannon, & S. H. Oh (Fagaceae), common name tanoak, has a reputation as a “difficult to work with” hardwood species that has been viewed at different times in history as everything from a valuable resource for edible acorns to an annoying “weed” tree that interferes with commercial forest management. This paper explores the complex character of the species from a wood products point of view and discusses the possibility of developing it as a valuable forest-products resource.

A comprehensive review of the forest-product literature reveals the many ways tanoak has been utilized. These uses have included fuel wood, lumber, railroad ties, flooring, and furniture, and as a source for leather- tanning chemicals. Early studies of the physical and mechanical properties of the wood show a similarity to many commercial hardwood species. However, tanoak has never gained the status of a preferred timber tree for forest products. This paper compiles what is known about the wood properties of tanoak and provides recommendations for successful lumber manufacturing. The risks and benefits of utilizing a species that is a known host for *Phytophthora ramorum* Werres, De Cock & Man in't Veld, the pathogen that causes sudden oak death, are also discussed from a forest-management point of view. As interest grows in developing local resources that require little transportation from source to end use, more opportunities for utilizing tanoak will likely emerge.

Key Words: California hardwoods, *Notholithocarpus densiflorus*, tanoak, wood drying, wood properties, wood utilization.

Notholithocarpus densiflorus (Hook. & Arn.) Manos, Cannon, & S. H. Oh (Fagaceae), common name tanoak, is a prevalent hardwood species in Oregon and California. It is an abundant tree in the Northern California forest, making up about 18% of the hardwood tree volume and 6% of the total tree volume in the state (Christensen et al. 2008). The species has a long history of use and abuse, and has suffered a bit of an identity crisis. Having features in common with both oaks (acorns) and chestnuts (flowers), it has had common names that have included one, the other, or both names, such as evergreen chestnut oak, California chestnut oak, tan bark oak, and tanoak. It is neither a chestnut nor an oak but has been classified in the genera *Pasania*, *Quercus*, and for most of the 20th and the first decade of the 21st century in the genus *Lithocarpus*. Tanoak is the only species of *Lithocarpus* native to North America; the other nearly 600 species of *Lithocarpus* are native to East and Southeast Asia (Govaerts and Frodin 1998). Recently, tanoak was classified in its own genus, *Notholithocarpus*—false *Lithocarpus* (Manos et al. 2008; Tucker 2012).

Over the years tanoak has been considered by many to be a unique and valuable tree species and by others a weed that should be eradicated. It was described by a well-known botanist in 1895 as “one of the most interesting inhabitants of the forests of the U.S.” (Sargent 1895), and a U.S. Forest Service forest-products researcher (Betts 1911) commented in 1911 that “there seems no good reason why tanbark oak [tanoak] should not provide for all the purposes for which eastern hardwoods are imported [from the eastern U.S. to the western U.S.]” More recently, a U.S. Forest Service research scientist (Bolsinger 1988) described tanoak as “aggressively tak[ing] control of sites after conifers have been removed in logging operations. ... [It is] considered a weed tree by timberland managers.” It is common for commercial timberland managers in California to resort to the use of herbicides to help control the vigorous sprouting and growth of tanoak (Tappeiner et al. 1987; Bowcutt 2011). Management techniques for controlling tanoak or managing for its wildlife, watershed, or forest-product value are beyond the scope of this paper, but good introductions to this topic can be found in

McDonald and Huber (1995) and Jensen et al. (1995).

Although the commercial value of tanoak as a resource for forest products has received mixed reviews, its high value to wildlife, forest diversity, and as a food source for Native Americans has long been understood (Stuart and Sawyer 2001). Historic uses of tanoak wood and bark have included fuel wood, a source of tannin for processing animal hides, and sporadically as construction lumber and flooring. Also, the Native Americans in California recognized early on that by grinding and leaching the tannins out of the acorns, a nutrient-rich food, high in complex carbohydrates (55–69%) was obtained. It is reported that the Hoopa of Northern California preferred tanoak acorns over the true oak acorns also available to them, and that one tanoak could annually provide about one pound of food supplement per day (Jackins 2004).

Tanoak was an important resource for the leather-tanning industry in California from the mid-19th to mid-20th centuries—this is actually the source of the tree's common name. Tannin is a natural chemical found in many plants that is used to tan animal hides. Willis Linn Jepson (1911) reported that the bark of the tanoak tree has a very high concentration—about 10–29% by weight—of a high-quality tannin preferred by the premium leather industry. Jepson also reported that at peak production in the early 1900s, about 30,000 tons of bark from 120,000 trees was harvested per year to supply about 100 tanneries—leaving behind about three million cubic feet of wood, which was left to decay in the forest as only the bark was used. At that rate of consumption the industry was considered sustainable, but with continued growth the decimation of the tanoaks near the tanneries would have left a marked impression on the diversity of the forest, not to mention the “stupendous annual waste of wood” (Jepson 1911). The tanning industry started using synthetic tannins in the early 1960s, leading to the eventual end of the tanoak-bark harvest.

From the mid-1900s forward, many researchers recognized the destructive, hazardous, wasteful, and unsustainable practice of peeling bark for the tannin industry and leaving good wood to decay in the forest. In addition to the tanoak's well-known value as firewood, products from heavy timbers to flooring, fine furniture, and even pulp for making paper were tested—resulting in adequate, if not superior performance. Yet none of these products has ever generated much interest in the industrial and manufacturing marketplace. Conservative estimates reveal that about one quarter of the 3.6 billion cubic feet of tanoak in the California forests—about 6% of total hardwood and softwood forest tree volume—is of saw-log size

and quality (Bolsinger 1988; Christensen et al. 2008). Harvesting only 1% of this volume would produce about 15 million cubic feet of sawn lumber for a California hardwood lumber market that is estimated to be about 150 million cubic feet in total (Shelly 1996; Laaksonen-Craig et al. 2003). A harvest of 15 million cubic feet is about 20% of the estimated annual growth of tanoak (Bolsinger 1988). This rudimentary analysis suggests that a sustainable harvest of tanoak could be a viable component of the California forest products industry (Shelly 2001).

An added benefit of harvesting tanoak could be the development of an infrastructure to provide a value-added alternative to managing diseased tanoak trees that are infested with the sudden oak death (SOD) pathogen, *Phytophthora ramorum* Werres, De Cock & Man in't Veld. Although the full impact of SOD on the mortality of tanoak across its range is not fully understood, evidence is mounting that a widespread decline of tanoak is taking place (Cobb et al. 2012). Having a viable market for tanoak wood products could provide the incentive needed to responsibly remove diseased trees from the landscape.

METHODS

The focus of this paper is to examine the wood properties and lumber quality of tanoak and to evaluate the potential to grow a tanoak forest-product industry. The argument presented is based on a comprehensive review of the literature that pertains to the known record of wood properties for tanoak. The effects that *P. ramorum* has on the wood properties and the potential to use the wood from diseased trees is summarized from a three-year project that involved monitoring the collection of about 1200 tons of woody debris from Marin and Santa Cruz counties that was heavily infested with the SOD pathogen (Shelly et al. 2005). A subset of this woody debris included 24 tanoak saw-logs from Santa Cruz Co. that were processed into kiln-dried, finished lumber, which was then evaluated for yield and quality.

RESULTS AND DISCUSSION

Wood Properties

The scientific interest in the properties of tanoak wood is centered around three time periods. The first recorded study occurred early in the 20th century (Betts 1911) at the peak of the California leather tanning industry. Interest in the species again peaked during the middle of the 20th century when the University of California Forest Products Laboratory focused on documenting the properties of the native California hardwoods (Paul et al. 1955; Randall 1956;

Schniewind 1958, 1960), and again at the end of the 20th century when communities began developing an interest in building small companies focused on local resources (Shelly 1996; Shelly and Jackovics 2001; Shelly et al. 2005). Results of these and similar studies consistently report wood-property values that place tanoak in the category of the densest (specific gravity), strongest (bending strength, modulus of rupture or MOR), stiffest (bending stiffness, modulus of elasticity or MOE), and hardest (hardness) woods of North America. Of the 113 commercial species listed in the Wood Handbook, only 19 have a greater average density (Ross 2010). This places tanoak in the same grouping as other high-density woods such as white oak, hickory, and locust.

Table 1 presents a summary of a selection of the wood properties reported in the various tanoak studies. The results are reported in two moisture-content (MC) categories, as the properties are dependent on the moisture content of the wood when tested. The mechanical properties of wood are typically measured at green moisture contents (above 30% moisture by weight as a fraction of the oven-dry mass, the nominal fiber saturation point) or air-dry moisture contents (12% MC). It can be risky to compare the results of studies done in very different time periods because of differences in test equipment and standards. For example, the comparatively low values for mechanical properties in the green condition reported by Randall (1956) could be explained by differences in experimental methods, or it could be related to sampling trees at the lower end of the expected density range for the species. Although not directly comparable, the results of all these studies are within the realm of the expected between-tree variation, and there is value in combining the results to create a composite average that then represents a greater geographic range of the trees being sampled (Table 2). Based on these results, tanoak is of similar density; is about 10–20% greater in strength, stiffness, and hardness; and is between 30–40% greater in shrinkage than northern red oak (*Quercus rubra* L.), which is used for comparison as a benchmark commercial species commonly used in hardwood manufacturing (Ross 2010). The greater mechanical-property values are beneficial, whereas the greater shrinkage is detrimental and emphasizes the importance of proper drying of the wood, which will minimize most problems associated with such high shrinkage values.

In addition to the mostly favorable comparison of tanoak wood properties to a benchmark commercial hardwood discussed above, other studies document favorable woodworking characteristics. Studies conducted at the USDA Forest Products Laboratory in the mid-20th

TABLE 1. COMPARISON OF SELECT TANOAK WOOD PROPERTIES FROM VARIOUS RESEARCHERS. *Based on density measured at oven-dry mass and green volume, nr – not reported.

Property	Specified moisture content condition	Study referenced				
		Betts 1911	Randall 1956	Paul et al. 1955	Schniewind 1958, 1960	Resch 1963 Shelly et al. 2005
Specific gravity*	od mass, g. vol.		0.54	0.581	0.574	0.55–0.60
MOR (lbf/in ²)	green	nr	8,866	10,470	10,140	nr
MOE (×10 ⁶ lbf/in ²)	green	10,110	1.32	1.55	1.88	nr
Side hardness (lbf)	green	1.68	947	nr	nr	nr
MOR (lbf/in ²)	air-dried	nr	16,300	nr	17,400	nr
MOE (×10 ⁶ lbf/in ²)	air-dried	16,000	1.80	nr	2.26	nr
Side hardness (lbf)	air-dried	2.1	1,400	nr	1,450	nr
Shrinkage (%)						
Radial	green to oven-dry	6	nr	4.9	6.3	nr
Tangential		12	nr	11.7	12.0	nr
Volumetric		18	nr	17.3	18.7	nr

TABLE 2. SELECTED, AVERAGE WOOD PROPERTIES FOR TANOAK COMPARED TO THE STANDARD VALUES FOR NORTHERN RED OAK, A BENCHMARK COMMERCIAL SPECIES.

Property	Specified moisture content condition	Average		Difference (%)
		Across studies	Northern red oak	
Specific gravity	od mass, g. vol.	0.57	0.56	1.4
MOR (lbf/in ²)	green	9,897	8,300	19.2
MOE (×10 ⁶ lbf/in ²)	green	1.6075	1.35	19.1
Side hardness (lbf)	green	947	1,000	-5.3
MOR (lbf/in ²)	air-dried	16,567	14,300	15.9
MOE (×10 ⁶ lbf/in ²)	air-dried	2.0533	1.82	12.8
Side hardness (lbf)	air-dried	1,425	1,290	10.5
Shrinkage (%)				
Radial	green to oven-dry	5.6	4.0	40
Tangential		12.4	8.6	44
Volumetric		18.0	13.7	31

century determined that tanoak exhibited good machining (Davis 1947) and gluing properties (Olson 1955) that compared favorably with other commercial hardwood species. Macroscopic and microscopic studies of tanoak describe it as a close-grained, diffuse porous wood with distinctive, large rays giving the wood an appearance similar to the true oaks (Schniewind 1958). These results, which collectively referred to tanoak as having “good workability,” are reinforced by much anecdotal evidence shared by woodworkers and manufacturers as summarized by Shelly and Jackovics (2001).

Appearance is an important characteristic for wood that is used for furniture, flooring, or other high-value uses where the look of the finished piece is important. Appearance is a subjective criterion that is hard to quantify. For example, the large rays found in tanoak are considered by

some consumers as a characteristic that should be emphasized, whereas others dislike the non-uniform appearance of large ray patterns (Fig. 1). Tanoak is also known to be susceptible to the formation of gray-brown stains during drying (Shelly and Jackovics 2001), which can add to the non-uniform appearance of the wood. These appearance issues can be minimized by following good milling and drying practices as discussed below.

Drying Characteristics

The importance of drying lumber to a moisture content compatible with the moisture conditions of its intended end-use environment is common knowledge. It is also well known that the ability to dry wood without causing serious degradation is not only a function of the manufacturing methods



FIG. 1. Appearance characteristics of tanoak wood (left—dark discoloration often found in center of mature trees, right—profile of broad tanoak rays on a quarter-sawn surface).

TABLE 3. RECOMMENDED DRYING SCHEDULE FOR TANOAK LUMBER.

Step	Wood moisture content (%)	Target conditions for the drying environment	
		Air temperature (F)	Relative humidity (%)
1	Green–50	70	55
2	50–30	80	60
3	30–25	100	85
4	25–20	110	70
5	20–15	120	50
6	15–8	140	40
7	8	140	55

and drying technique used but is also highly species dependent. Tanoak is known as a “difficult to dry” wood species (Espenas 1953; Resch et al. 1963; Shelly 1995). Tanoak has a tendency to develop excessive cell collapse, warp, and wood discoloration (stain) if not dried properly (Shelly and Jackovics 2001). The excessive cell collapse is especially problematic in the dark-colored zone of wood often found in the center of older trees (Fig. 1). This zone is independent of the juvenile and heartwood zones of trees and thought by some to be related to biological degradation (Prestemon 1967). Tanoak also exhibits more shrinkage in each of the three ordinal directions of lumber (tangential and radial to the growth rings, and longitudinal to the axis of a tree) than northern red oak (Tables 1 and 2). Shrinkage factors of 30–40% greater than the expected shrinkage for northern red oak (Table 2) is a cause for concern that emphasizes the necessity of following manufacturing practices known to help minimize shrinkage-related problems, such as the careful selection of sawing patterns (e.g., quarter-sawn) and drying practices that improve dimensional stability (Shelly and Jackovics 2001).

A review of drying methods developed by other researchers combined with the results of a tanoak manufacturing study reported by Shelly and Jackovics (2001) led to the development of the recommended drying schedule for tanoak lumber presented in Table 3 (Shelly 2005). In these studies, it was confirmed that the control of drying conditions during the early stage of drying is the most important factor in achieving high quality, dry lumber—a practice often followed with other difficult-to-dry hardwood species such as white oak (*Quercus alba* L.). It was determined that careful air drying at temperatures below 80°F—combined with high rates of air flow to quickly remove surface water away from the wood—can reduce the number of boards with severe cell collapse from 20% of the total to 2%, and the boards with severe stain from 30% to 5%. These results, combined with experiential evidence of practitioners, led to the development of the following recommended practices for producing high-quality tanoak lumber.

1. Avoid cutting lumber from the dark-colored core of the log—excessive collapse cannot be avoided in this zone;
2. Saw to maximize the amount of quarter-sawn lumber;
3. Stack lumber to dry in uniform piles with aligned stickers and a top-load restraint of at least 150 lbs per sq ft;
4. Encourage rapid initial drying of the surface at temperatures below 80°F to minimize kiln stain;
5. Air-dry to an average moisture content of about 35% (which will take four to nine months—depending on drying conditions);
6. Kiln dry to 8% moisture content following the mild kiln schedule presented in Table 3.

Impact of Sudden Oak Death

Tanoak, being a major host for *P. ramorum*—the sudden oak death pathogen, raises special utilization concerns. First, there is concern that harvesting tanoak trees, transporting logs, and processing wood may increase pathogen spread. And second, the wood of *P. ramorum*-infested trees may be too degraded to be acceptable for most potential products. Shelly et al. (2005) studied these issues and determined that the risk of spreading the pathogen through processing was very low. They found that even though the quality of lumber produced was degraded, the majority of the deterioration was in the outer one inch of the logs and that high-quality lumber could still be produced. It was also noted that lumber cut from the deteriorated zone (where it had been attacked by wood-boring beetles and exhibited early signs of wood decay) produced wood having a distinctive appearance. This type of wood (i.e., “spalted wood”) is often valued as a premium product by woodworkers.

Lumber Yield

Two important considerations in evaluating the commercial success of producing lumber from any tree species are the quantity and quality of lumber that can be manufactured following

TABLE 4. PERCENTAGE TANOAK LUMBER YIELD BY PROCESSING AND QUALITY CATEGORY. a: Dickinson and Prestemon 1965; b: Shelly and Jackovics 2001; c: Shelly et al. 2005.

Quality	Un-infected by SOD			Infected by SOD	
	Green ^a	Green ^b	Kiln-dried ^b	Green ^c	Kiln-dried ^c
High	12.9	22.5	12.1	12	10.8
Moderate	40.4	48.0	55.2	44	27.3
Low	39.7	29.5	32.7	39	55.8
Cull	6.9	0	0	6	6.1

conventional milling and drying. Two studies, conducted 36 years apart, reported such data from tanoak-processing mill studies (Dickinson and Prestemon 1965; Shelly and Jackovics 2001). It is difficult to compare results from studies conducted decades apart as they likely used different processing equipment and measurement protocols. However, the results of these two studies are similar and provide the best information available on expected lumber yields.

The yield of green (not dried) lumber reported by Dickinson and Prestemon (1965) was estimated at 65% of the log volume, whereas Shelly and Jackovics (2001) reported 55% green-lumber yield. One possible explanation for the difference is that the first study selected higher-quality logs, while the second used mill-run (ungraded) logs that undoubtedly had the higher losses typical for lower-grade logs due to the higher incidence of defect zones (not SOD related). The first study only determined the volume yield of green lumber. The second also recalculated yield after the lumber was kiln-dried, taking into account the volumetric shrinkage during drying. Lumber yield after kiln drying was reduced to 46% of the original log volume. The results of these volume yield studies are similar to, but on the low side, of the accepted hardwood industry norm of about 50–60% dry-lumber yield.

The two studies cited above also provide data on the quality of lumber expected from milling tanoak logs. In order to make it easier to compare the results of these different studies, the quality categories of high, moderate, low, and cull (unusable) were used, as shown in Table 4. These categories are roughly equivalent to the National Hardwood Lumber Association lumber grades as follows: high is FAS, moderate is No. 1 Common, low is No. 2 Common, and cull is No. 3 Common. The results are in agreement with hardwood-industry expectations of producing about two-thirds of the lumber in the upper grades (high plus moderate). However, the drop in quality associated with kiln drying was greater than expected. At most, a 10% shift from high grade to moderate grade because of kiln-drying defects would typically be expected, but Shelly and Jackovics (2001) reported a 46% drop. This excessive loss of the highest-quality lumber stresses the importance of the kiln-drying operation and of following the

drying schedule (Table 3) recommended by Shelly and Jackovics (2001).

The impact of *P. ramorum* on lumber yield and quality was studied by Shelly et al. (2005) in trees that had succumbed to SOD. As seen in Table 4, lumber quality was dramatically reduced in infested logs. After kiln-drying, only 38% of the lumber remained in the upper grades. Such a reduction in quality would seriously jeopardize the economic viability of a sawmill operation working only with infested trees. A possible solution to reducing this impact is to develop a management plan that identifies diseased trees for milling before major deterioration has occurred.

Potential Uses

Tanoak has at one time or another been used successfully in a wide variety of products. These include tannin, acorn meal, fuelwood, railway ties, truck and railcar flooring, mine timbers, dunnage, flooring, furniture, and paper pulp. These continue to be viable product options for tanoak. Low-quality tanoak biomass is also used in California as a component of biomass fuel for biomass power plants. It also has the potential to become a feedstock for chemical production including transportation fuels. Higher-quality tanoak resources are perhaps best suited for value-added wood products (Fig. 2). For example, a small sawmill in Santa Cruz Co., California has, for more than a decade, been harvesting, sawing, and kiln-drying tanoak lumber to produce hardwood flooring (Fig. 3).

SUMMARY

Tanoak is unlikely to ever be harvested in large enough quantities to displace a commodity hardwood lumber such as red oak, but many opportunities exist to create local or niche markets that emphasize its many positive attributes. A comprehensive review of tanoak studies revealed that many of its wood properties are comparable, and in some cases superior, to popular, commercial hardwood species. But these studies also identified processing concerns that need to be addressed in order to sustain an economically successful enterprise. Recent studies that focused on the drying properties of tanoak



FIG. 2. Example of products produced from tanoak lumber (left—hardwood flooring, right—hand-hewn bench).

offer recommendations that minimize drying defects and increase the chances of operating a successful business. Emphasizing the special character and unique appearance of tanoak was also discussed as a positive marketing tool.

Recent studies also confirm that lumber can be produced from *P. ramorum*-infested tanoak trees, but at a diminished value compared to healthy trees. For sawmilling to be a viable management option in areas with SOD, it is absolutely necessary to follow the best manufacturing practices and understand the inherent risks associated with tanoak, such as excessive shrinkage and the strong tendency to develop drying defects. These recommended practices include sawing logs in order to avoid any dark-colored core wood and maximize quarter-sawn lumber, stacking the lumber properly, using top-load

restraint, and following the mild-drying schedule presented in Table 3.

Tanoak is a resilient forest species with many attributes and one that can be effectively managed to create a sustainable utilization strategy. Harvesting tanoak trees contributes to management strategies for controlling *P. ramorum* by creating a market for infested wood, thus removing some of the pathogen load from the forest and reducing the hazards associated with dead trees, especially in the wildland/urban interface. Opportunities also exist to expand the tanoak product market by focusing on the consumer preference of buying value-added products made from local resources by local producers. These attributes are recognized as positive benefits to growing the market for tanoak products.

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FIG. 3. Tanoak lumber stacked and ready for loading into a low-temperature, forced-convection, lumber dry kiln at a small mill operation in Santa Cruz Co., California.

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FOODS FROM THE TANOAK FOREST ECOSYSTEM

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ABSTRACT

This paper offers a modern take on wild edible plants of the tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), ecosystem with instructions for gathering materials and preparing foods. We review the collection and processing of acorns, bay nuts, and foliage for herbal teas, along with specific recipes.

Key Words: Acorns, edible plants, medicinal tea, tanoak, wild foods.

The tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), ecosystem has produced an abundance of food for wildlife and native people for millennia. The recent resurgence in foraging for edible wild plants boasts potential benefits to the health of people as well as our planet. As described by Andler and Feinstein (2011), wild plants are the most natural, whole food one can eat, and generally more nutritious in terms of vitamins, minerals, and antioxidants—all those micronutrients that the plants develop in order to protect their own health in the absence of chemical fertilizers, pesticides, and genetically modified seed. Moreover, eating local wild plants can contribute to a more sustainable food system by cutting back on water usage and transportation costs, as well as not requiring the levels of outside inputs that modern agriculture relies upon (Andler and Feinstein 2011).

When collecting wild foods, caution is needed; there is a definite distinction between contributing to a more sustainable food system and depleting a resource. Sustainable harvesting techniques need to be practiced whenever harvesting wild edibles. Some general guidelines include harvesting a plant if it is clearly growing in abundance and only harvesting up to a third of that plant's entire mass (Andler and Feinstein 2011). In addition, traveling through different forests, potentially off-trail and in sensitive areas, requires great care so as not to inadvertently spread insects, pathogens, and weeds. Following simple sanitation techniques (COMTF 2006) to reduce the spread of these pests will help keep our forests free of damaging invasive species. A full set of gathering ethics can be found in Peters and Ortiz (2010).

Following is a modern take on gathering and preparing wild edible plants of the tanoak ecosystem.

ACORNS: FROM TREE TO TABLE

A mature oak (*Quercus* spp. as well as tanoak, *Notholithocarpus densiflorus*) can produce almost

1000 pounds of acorns in one growing season during normal weather conditions in a good year—which usually occurs every four to five years (Ortiz 1991). Acorns made up half of the diet of many native Californians (Heizer and Elasser 1980), and local native elders prized tanoak and black oak acorns especially for their flavor and nutritional value (Peters and Ortiz 2010). Acorns are high in fiber, low in sugar, lower in fat than most nuts, and are noted for controlling blood sugar levels and maintaining a healthy body weight. A reliable source of carbohydrates, protein, 6 vitamins, 8 minerals, and 18 amino acids, acorns are more carbohydrate than protein, and functionally more like a grain than a nut (Andler and Feinstein 2011). They have a sweet, mildly nutty flavor when properly prepared. Acorn flour may be used in bread recipes, substituting acorn flour for approximately 1/4–1/2 of the wheat flour. Acorn meal can be used in place of nuts in cookie, brownie, and bread recipes, and in place of corn meal in most recipes (Bainbridge 1986).

Acorns have high levels of tannins which need to be removed before human consumption, as they are toxic to humans in large amounts (Clay 2003; Andler and Feinstein 2011). While different oak species contain varying levels of tannins, virtually all of the acorns eaten by native Californians contain high enough levels of tannins to require leaching.

General Guidelines for Processing Acorns

Depending on location, type of acorn, materials accessible, and personal practice, many variations in acorn processing methods exist. We refer to “Acorns and Eat ‘Em” (Ocean 2001) for the following guidelines, and suggest further research and individual experimentation with acorn processing to create a personal processing practice that works best for those interested. Below are some general guidelines.

1. **Harvesting acorns:** Acorns can be harvested as soon as possible after the second crop of the season falls off an oak tree. The first fall consists largely of worm- and insect-infested acorns, and is not suitable for use. The second fall consists of healthy nuts brought down by wind usually in late September and October (Ortiz 1991). Acorns for collection may be green, green and tan, or brown. Although the green nuts aren't fully ripe, they will continue to ripen and turn dark brown in a few days.
2. **Drying:** Spread acorns on a tray or screen. Discard any acorns with signs of mold or worm holes. Dry the acorns either in direct sunlight for 2–5 consecutive days or in a warm 175°F oven for 20 min with the oven door slightly ajar to allow moisture to escape. You can also dry acorns in a box in a warm area (e.g., near a stove) over the course of a month, as long as you regularly stir them to prevent mold development (Peters and Ortiz 2010).
3. **Storage:** After reinspection for mold or holes, store dried acorns in a cool dry place out of direct sunlight. Acorns can keep for several years if properly stored. A variety of storage containers may be used, ranging from burlap sacks to kitchen bowls or jars; there is a general consensus to avoid plastic since they may pick up plastic flavors.
4. **Opening the outer shell:** Remove the acorn nutmeats from their outer shells when you are ready to process and eat them. Crack the thin outer shell with a nutcracker. Peel it off, saving the inner nutmeat, which can then be processed either whole or ground into a coarse meal.
5. **Leaching:** Acorns have reportedly been leached by a variety of methods. Whichever you choose, it is important to taste a small amount to determine if the tannic acid has been sufficiently removed—it should taste sweet and may require more leaching if still bitter. Acorns may be leached by placing in hot water for an hour, draining, and repeating the process a few times; by flushing with running, cold water continually for several hours; or by soaking in water that is changed daily for a week. All these methods remove the water-soluble tannic acid. Ocean (2001) recommends the third method, blending the acorns first with water in a ratio of 3 parts water to 1 part acorns, and then placing the mixture in large jars in the refrigerator, where the meal will settle to the bottom. Each day, pour off the water darkened by the tannins and add fresh water.
6. **Using processed nuts:** Once leached, the damp acorn nutmeat may be used in a variety of recipes, or dried (either by the

sun or in an oven) for later use. Pound or grind dried nutmeats to desired consistency. Acorn grits and flour will keep in a sealed container for several weeks in a refrigerator or several months in a freezer. Since it contains oil, ground meal will turn rancid if left in a warm environment. Whole acorns dried in the shell may last for several years.

CALIFORNIA BAY LAUREL: LOCAL COFFEE-CHOCOLATE

The nuts of the California bay laurel, *Umbellularia californica* (Hook. & Arn.) Nutt. (Lauraceae), are edible when roasted and have long been consumed by California tribes as a condiment, digestive aid, and stimulant. Many people would eat bay nuts in spring or fall to ready the body for seasonal changes (Andler and Feinstein 2011). Plain bay nuts taste like a cross between a coffee bean and cacao bean, and are quite pleasant mixed with a little sweetener such as honey or agave nectar. You can also grind the nuts in a coffee grinder and steep the powder in hot water to make a cross between coffee and hot chocolate (again, this is recommended sweetened) or use the powder as you would cacao powder. Bay nuts contain a chemical constituent similar to caffeine; their stimulating effects have been described as edgier than caffeine, but shorter lived (K. Feinstein, naturalist, personal communication). The nuts contain 40–60% of a waxy fat which behaves very much like cocoa butter (K. Feinstein, personal communication).

Processing Bay Nuts Step-by-Step

1. **Harvesting.** Bay nuts are harvested in the fall (October through November), when they drop from the trees. Select nuts that have not sat on the ground too long, judging by the condition of the fleshy outer husk.
2. **Peeling.** Peel off the outer fruit from the nuts soon after harvesting, before the variously colored fleshy coatings begin to wither and rot (Fig. 1). When fully ripe, just as the outside begins to turn purple, the fruit may be eaten like an avocado, but the window is quite narrow between unripe (bitter) and overripe (rotten), and usually the fruit must be discarded.
3. **Drying.** Dry the peeled nuts in their shells on a baking sheet in the oven at 350°F for about 10–15 minutes—or until they start to crack open. The nuts can keep for about a year once fully dried (Peters and Ortiz 2010).
4. **Roasting.** Crack the shells open with a nutcracker. Inside you will find the near-translucent, beige-colored nutmeats that easily break in half, similar to peanuts. Place the



FIG. 1. Peeled bay fruit reveals the nut inside.

nutmeats on baking sheets roast for 30–45 minutes at 350°F, stirring occasionally—approximately every ten minutes. If roasting at higher temperatures, up to 450°F, you may need to stir them every few minutes. Bay nuts can cross from underdone to overdone quickly, and should be checked frequently. The bay nuts will turn darker shades of brown, from tan to the color of milk chocolate to dark chocolate, and eventually to a black-brown (overdone); a tasty roasted bay nut is a dark chocolate brown. The essential oils remaining in bay nuts that have not been roasted long enough make them pungent and inedible, whereas if roasted until too dark, the nuts become bitter and reminiscent of charcoal. Remove from the oven as soon as the average nut is similar in color, approximately the shade of coffee with cream.

5. Storage. Roasted bay nuts can be stored in an airtight container at room temperature for several months.
6. To serve. Mix roasted nuts with local honey (such as tanoak honey, if available) and a sprinkling of sea salt.

HERBAL MEDICINES: DOUGLAS-FIR AND YERBA BUENA TEAS

Douglas-Fir

The young shoot tips of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae), have a subtle woody, slightly astringent flavor, and can be eaten raw. They have also been used as a flavoring in cooked foods. A refreshing tea is made from either the young or mature needles that is rich in vitamin C and has been used in the treatment of colds. It is said to have expectorant

qualities as well (The Living Wild Project 2011) and has been used as an inhalant in steam baths.

To make Douglas-fir tea, harvest the bright green needle tips in the springtime—March through May. The darker mature needles may be used as well, and have a slightly more potent flavor. Remove the needles from the stems and finely chop or thoroughly bruise them, to release the essential oils. Alternatively, dry the needles to store for later use. Steep the needles in boiling water for 15–30 minutes, strain, and serve.

Yerba Buena

Native to North America, yerba Buena, *Clinopodium douglasii* (Benth.) Kuntze (Lamiaceae), is a common ground-cover in tanoak ecosystems. Yerba buena has been used medicinally for centuries; its positive health effects inspired Spanish colonizers to refer to it as the “good herb” or “*yerba buena*.” A member of the mint family, it shares many of the medicinal qualities of other mints, including the ability to counteract harmful microbes. Yerba buena tea is used to treat coughs and colds due to its expectorant qualities and as a digestive aid (Peters and Ortiz 2010). Due to its analgesic qualities, direct application of the herb as well as the juice from crushed leaves is used as a pain reliever for headaches, toothaches, and insect bites (Medicalhealthguide.com 2012).

Yerba buena tea can be made from either fresh or dry leaves. Dry the leaves on a tray for a few weeks in a warm dry area, or in a dehydrator. Steep fresh or dry leaves in boiling water for up to 30 min.

ACKNOWLEDGMENTS

The recipes outlined in this paper were used to create an exhibit of native plant foods at the “Tanoak Wild” session of the Fifth Sudden Oak Death Science

Symposium in Petaluma, CA on June 22, 2012. Participants were able to view the foods at different stages of processing (i.e., whole nuts, ground flour, etc.) and sample the finished products. Thank you to Spencer Nielsen for foraging for bay nuts, Douglas-fir and yerba buena, as well as his knowledge and assistance in wild food preparation. Many thanks to three anonymous reviewers for their helpful comments and to Victoria Jimenez for her editorial assistance. This work was funded by a grant from the American Recovery and Reinvestment Act (ARRA) provided by the USDA Forest Service and California Department of Forestry and Fire Protection (CAL FIRE).

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GENETIC STRUCTURE OF *NOTHOLITHOCARPUS DENSIFLORUS*
(FAGACEAE) FROM THE SPECIES TO THE LOCAL SCALE: A REVIEW OF OUR
KNOWLEDGE FOR CONSERVATION AND REPLANTING

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ABSTRACT

Tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), is an important component of mixed-evergreen forests and woodlands in coastal California and Oregon, with incursions into the Sierra Nevada and the Klamath Ranges. Sudden Oak Death (SOD) is causing severe dieback and mortality in tanoak and could transform these ecosystems in areas where the pathogen *Phytophthora ramorum* S. Werres, A.W.A.M. de Cock can become established. Knowledge of genetic diversity within the species is important for both disease resistance screening, conservation and replanting in sites with high mortality. Here we review what has been learned about the genetic structure within tanoak since SOD has caused disease epidemics in the species. We review published work on genetic structure at the species level and provide some re-analyses of these data that show divergence across the geographic range. We also review recently published data on genetic structure at a fine spatial scale that provides some guidelines for the selection of trees as seed sources. Finally, we interpret a range of seed provenancing strategies in the light of our knowledge of tanoak genetic diversity.

Key Words: Conservation, fine-scale genetic structure, genetic divergence, *Notholithocarpus densiflorus*, replanting, tanoak.

Human-induced perturbations as a result of resource use, habitat fragmentation and climate change are leading ecosystems to functional tipping points with potentially far-reaching consequences (Barnosky et al. 2012). In forested ecosystems, the fine balance between a functioning system in which hosts and pathogens co-exist and the rapid decline that ensues when environmental conditions push the system out of equilibrium is an example of such a tipping point. Recently, this has been exacerbated by the movement of organisms globally, resulting in exotic diseases with catastrophic consequences. Forest trees are particularly vulnerable because of long generation times and sedentary life histories, but they are also critically important as keystone species of the broader ecosystem. Over the last century, several forest tree diseases have caused such severe host mortality that, what were once

keystone species have been threatened or reduced from overstory trees to understory shrubs. Chestnut blight is a notable example on the American continent (Garnas et al. 2011) and pandemics of Dutch elm disease have been catastrophic across the northern hemisphere (Brasier and Buck 2002).

The current epidemic of Sudden Oak Death (SOD) caused by the exotic pathogen *Phytophthora ramorum* S. Werres, A.W.A.M. de Cock has a very wide host range and is shaping up to be a potentially devastating disease on tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), in central and northern California (Rizzo et al. 2005). Epidemiological risk analyses suggest that, like other systems, tanoak forests are likely to be transformed through the loss of overstory trees and may only avoid extinction through successful

resprouting (Cobb et al. 2012). If the disease takes the course predicted by Cobb et al. (2012), replanting will be necessary to augment genetic diversity that may be lost stochastically as stands regenerate vegetatively and to re-introduce diversity in stands that fail to resprout. Selection of suitable seed sources will be critical to the conservation of genetic resources as well as for successful replanting. There is considerable debate as to the optimum strategy for selecting seed sources that will maximize the likely success of local populations, while promoting a diverse gene pool on which selection can act if environmental conditions change (Breed et al. 2012). Seed collection from local sources to maximize likely locally-adapted genotypes may lead to inbreeding depression if population sizes have fallen below a threshold level (Eckert et al. 2010; Breed et al. 2012), whereas mixing seeds from different geographic sources introduces the risk of outbreeding depression if the source populations are from different locally adapted gene pools (Kramer and Havens 2009). Reciprocal transplant studies are helpful to gain some insights among these competing scenarios. However, for many tree species, such approaches are too time-consuming, so molecular marker data need to be used. Molecular methods allow the rapid documentation of genetic diversity, but in most cases sequences of DNA, or analyses of DNA fragment sizes are confined to regions of the genome that are not transcribed and are assumed to be selectively neutral. Although such DNA markers do not necessarily indicate genetic adaptations, they do provide us with information on evolutionary divergence that would indicate zones for conservation management (Moritz 1999) and seed sources that should not be mixed for planting if outbreeding depression is a concern.

Spatial organization of genetic diversity is a property of species that derives from contemporary demographic processes and past environmental events. At a broad spatial scale, encompassing a range of environmental conditions, evolutionary forces operate on the different gene pools and can lead to more or less divergent lineages (Hampe and Petit 2005). Detecting genetically divergent groups of individuals or populations is an area of interest in evolutionary biology (Pritchard et al. 2000; Manel et al. 2003; Waples and Gaggiotti 2006) and has consequences for the evolutionary trajectory of host responses to disease (Parker and Gilbert 2004) and for designing appropriate conservation programs (Grivet et al. 2008). At a local scale, genetic structure varies as a result primarily of the balance between dispersal and stochastic processes of chance representation of alleles (genetic drift). Knowledge of fine-scale genetic structure (FSGS) provides information on the spatial

organization of pedigrees and the effective limits to recent seed and pollen dispersal. The latter can be important in resistance screening, where sampling of relatives may be desirable and in conservation and restoration where maximizing for genetic diversity in seed selection is the goal.

We have been studying genetic diversity in tanoak, with a view to understanding partitioning of genetic diversity at the broad (Nettel et al. 2009; Dodd et al. 2010) and fine-scale landscape levels (Dodd et al. 2013). Here, we review these earlier reports, re-analyze some of our earlier data with new tools and discuss the consequences for conservation and replanting strategies in the face of mortality from disease outbreaks. We refer to replanting rather than restoration because we are not proposing strategies to restore the ecosystem to its former state, but we are looking specifically at replanting of tanoak in areas where it has been lost through perturbations such as SOD.

THE SPECIES

Tanoak (*Notholithocarpus densiflorus*) was recently attributed to its monospecific genus by Manos et al. (2008) in recognition of its closer affinities to *Quercus*, *Castanea* and *Castanopsis* than to the Asian stone oaks (*Lithocarpus* spp.). Tanoak is a restricted endemic to the California Floristic Province; the tree form, *N. densiflorus* var. *densiflorus* ranges from disjunct stands in Ventura County, California to more continuous stands as far north as Coos County, Oregon (Tappeiner et al. 1990). Although it is best represented in the Coastal Ranges, it extends inland to the foothills of the Sierra Nevada. The dwarf form, *N. densiflorus* var. *echinoides* is more common at higher elevations in the north-eastern range of the species, particularly on serpentine. Occurrence reports of the dwarf form should be treated with caution as there is likely to be confusion over ecological dwarfism and genetically distinct forms (Dodd unpublished data). Tanoak is predominantly insect-pollinated (see Wright and Dodd this volume) and can produce heavy crops of acorns that have a relatively high viability; in addition it is a prolific basal sprouter.

GENETIC STRUCTURE AT THE SPECIES LEVEL: CONSERVATION UNITS

In defining management units for conservation under the pressures of climate change, Moritz (1999) argued for the greater importance of preserving distinct lineages over phenotypic or adaptive traits: while adaptations can be recreated given an adequate gene pool, historical processes cannot be repeated. Neutral genetic markers have been used extensively to detect lineages that have resulted from an overlay of

past events on biogeographic processes. Today, one of the greatest problems facing conservation geneticists is how to determine what constitutes distinct population lineages. In plants, chloroplast and nuclear genomes are the most commonly studied, but they may show distinctly different underlying patterns. Maternal inheritance of chloroplast DNA in most angiosperms commonly results in very strong geographic structure, particularly for heavy-seeded genera with short dispersal distances such as *Quercus* (Dodd et al. 2008; Grivet et al. 2008) and *Notholithocarpus* (Nettel et al. 2009). On the other hand, bi-parental inheritance of nuclear DNA results in much weaker geographic structure, as a result of large amounts of pollen with much greater dispersal distances than seed.

In tanoak, Nettel et al. (2009) detected four major and two rare chlorotypes based on four chloroplast microsatellite repeats (cpSSR) and one sequence region. No additional chlorotypes were detected in more extensive sampling of the species, particularly to the northern limit of its range in southern Oregon (Dodd et al. 2010). The four major chlorotypes included: 1. A coastal California type from Santa Barbara to Humboldt County, 2. A northern type from Humboldt County to the northern limit of the range in southern Oregon, 3. A Klamath Mountains chlorotype and, 4. A Sierra Nevada chlorotype (Fig. 1). Therefore, the chloroplast genome in tanoak displays a well-defined geographic structure, but low variation compared to California Floristic Province endemic oaks, such as coast live oak (*Quercus agrifolia* Née), for which we have detected 31 chlorotypes (Dodd et al. 2008) and valley oak (*Q. lobata* Née), for which 22 chlorotypes were detected (Grivet et al. 2008). However, comparisons among species should be treated with caution because of potential variations in diversity at the selected gene loci. Although the geographic partitioning is informative on barriers to seed dispersal, it does not mean that seed dispersal can occur throughout the geographic range of a chlorotype. Analysis of more of the chloroplast genome could reveal further variation within any of the four major types detected. Perhaps the most interesting finding from these results is the marked break between the northern and southern coastal types near Arcata, CA (Humboldt County) and the divergence between coastal and interior populations of tanoak. The former split is of greatest interest for SOD outbreaks and suggests northern and southern coastal lineages that have been separated and only recently come into secondary contact. Whether the two lineages differ in their tolerance to *P. ramorum* remains to be seen, but preliminary data do suggest low, but significant variation among populations (not including the

northern coastal chlorotype) in response to inoculation (Hayden et al. 2011).

Do Nuclear DNA Markers Support Divergence Revealed By The Chloroplast Genome?

As for other members of the Fagaceae (Sork et al. 2010), only weak genetic structure was detected among populations of tanoak (Nettel et al. 2009). This is generally interpreted to be a result of widespread pollen dispersal in many trees species (Ashley 2010). Field sampling for phylogeographic studies is commonly designed to cover the range of distribution of the species and to capture any potentially, naturally isolated groups of individuals. Unfortunately, although sampling locations are commonly referred to as populations, there is no a priori knowledge of what constitutes a genetic population, often interpreted as a panmictic group (but see Palsbøll et al. 2007), which then becomes a problem of post hoc inference. To infer panmictic groups, Nettel et al. (2009) used the Bayesian approach implemented in STRUCTURE (Pritchard et al. 2000). However, it is well accepted that when genetic structure is weak, the program STRUCTURE does not perform well in detecting the number of groups. An alternative Bayesian analysis BAPS performed on a larger data set, including more extensive sampling in southern Oregon, detected nine clusters (Dodd et al. 2010). However, although the BAPS assignments indicate spatially consistent grouping of populations, they do not show the relative importance of the partitions.

Here, we have extended our analyses using the software Barrier vs. 2.2 (Manni et al. 2004). The advantage of this analysis is that a hierarchy of importance of discontinuities and their direction on the landscape can be inferred. Barrier uses central coordinates for a sampled population first to calculate a Voronoi tessellation and then a Delaunay triangulation that draws a network connecting all the sample localities. The Monmonier's (1973) maximum-difference algorithm then takes a distance matrix (genetic distance) to identify boundaries, where differences between pairs of populations are greatest. The significance of these barriers can be tested by bootstrapping the distance matrix after re-sampling genotypes in each population. We used the population comparisons option in Arlequin 3.5.1.3 (Excoffier and Lisher 2010) to obtain a matrix of population pairwise genetic distances (Slatkin's linearized F_{ST}). To bootstrap distance matrices, we first re-sampled genotypes with replacement 100 times in each of the populations using the Excel add-in provided by Resampling Stats, Inc., Arlington, Virginia, USA. We then re-calculated the matrices of population pairwise Slatkin's linearized F_{ST} for each of the 100 re-sampled data sets. We ran Barrier to detect the locations of the first five

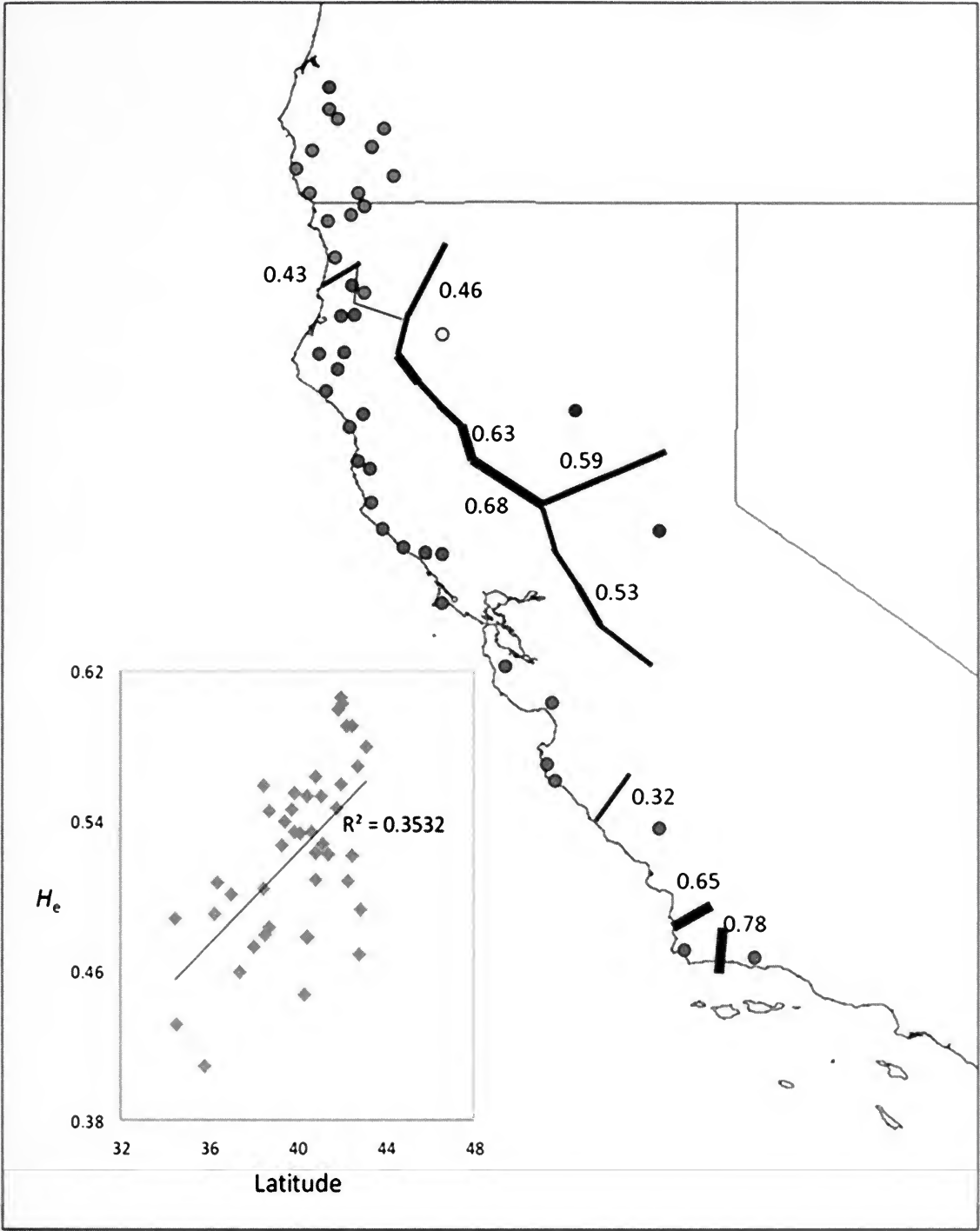


FIG. 1. Map of chloroplast and nuclear DNA breaks in the distribution of tanoak (*Notholithocarpus densiflorus*). Filled circles show sampling locations with colors depicting different chlorotypes (adapted from Dodd et al. 2010). Lines show the major breaks in nuclear DNA from BARRIER analysis of population pairwise Slatkin's linearized F_{ST} conducted in this report. Thickness of line segments are proportional to the ratio of F_{ST} of that segment to maximum F_{ST} . Numbers next to thickest line segments show proportional bootstrap support after resampling 100 times within populations. Inset shows relationship between expected heterozygosity (H_e) and latitude of origin of population (adapted from Nettel et al. 2009).

barriers in the genetic distance matrix and used the resampled data to determine bootstrap support.

The breaks detected by Barrier are shown in Figure 1 as lines of variable thickness corresponding to the ratio of the F_{ST} for each line segment divided by the maximum F_{ST} detected, as recommended by Manni et al. (2004). For clarity, bootstrap support values are shown only for the thicker line segments for each of the breaks. Interestingly, the first two barriers detected were in the southern range of tanoak between Santa Barbara and Lompoc and between Lompoc and Nacimiento respectively. Both of these breaks received strong bootstrap support. The third barrier separated interior populations from the Klamath Mountains and the Sierra Nevada from Butte County from coastal populations. The thickness of these segments tended to decrease northwards indicating a weaker divergence northwards, consistent with our earlier STRUCTURE analyses that grouped these populations with the northernmost coastal California group of populations and those from Oregon (Nettel et al. 2009). Interestingly, the Barrier analysis detected divergence between Sierra Nevada populations from Butte and El Dorado Counties. The fourth barrier continued the separation of interior and coastal populations southwards, with the greatest divergence between the El Dorado County population and those from the San Francisco Bay Area. The thickness of the segments decreased northwards as this barrier joined the third barrier and also decreased southwards. The fifth break that was detected separated north coastal and south coastal populations east of Arcata, California (Humboldt County). Notably, this barrier passed between two nearby populations from Korb and Hoopa (Humboldt County), consistent with the partition between the northern and southern coastal chlorotypes shown in color in Figure 1.

These new analyses of nuclear DNA support the divergence between coastal and interior populations and between north and south coastal populations detected from chloroplast DNA. In addition, they reveal probable isolation and fragmentation in the southernmost range of the species that was not evident from the chloroplast data.

What Can We Infer From Divergence?

Following Moritz (1999), we are looking for divergent lineages that have arisen because of past events; the most important for many plant taxa were the glacial cycles that have occurred over the last approximately 2 million years and the more recent Holocene warming. The major divergences in population lineages in tanoak do suggest correlations with these past events. The southern range of tanoak has likely been most

influenced by changes to a drier climate in the late Holocene (Kirby et al. 2007). Indeed, Nettel et al. (2009) inferred decreases in effective population size since the mid-Holocene. Today these populations are fragmented and relatively small and represent the trailing edge of the species. Genetic diversity, measured as expected heterozygosity, is least in these southern small and fragmented populations and increases northward (Fig. 1). Divergence across the Great Central Valley of California is not unexpected. Many taxa display deeper divergence between the Sierra Nevada and Coastal Mountain Ranges than within the mountain ranges, although this tends to be less clear for tree species (Calsbeek et al. 2003). However, it was surprising that a barrier was detected within the Sierra Nevada Range, between the Butte County and El Dorado County populations. More extensive sampling is needed to confirm this. Finally, the divergence between north coastal and south coastal populations shown most clearly with chloroplast DNA, and supported by nuclear DNA, shows a remarkable delineation over a very short distance. Indeed Dodd et al. (2010) reported only one population in which they found a mixture of the two chlorotypes. The most likely explanation is that climatic changes in the past resulted in restriction of tanoak north and south of this region that has only very recently become a zone of secondary contact. Taken together, the chloroplast and nuclear data suggest that the range of tanoak can be divided into at least four groups that should be considered in conservation efforts: 1. A northern group from Arcata to Oregon, 2. A northern and central California coastal group from Arcata south to Monterey County, 3. One or more interior groups (additional population sampling is required to determine the limits of these lineages) and 4. Two or more trailing edge populations in the southernmost range of the species.

WITHIN POPULATION GENETIC STRUCTURE: SEED SOURCES FOR REPLANTING

Conventional thinking dictates that local seed sources for replanting should provide gene pools that are well-adapted to the local environment (Broadhurst et al. 2008; Kramer and Havens 2009). However, severe mortality from disease may lead to drastic reductions in effective population sizes, with consequent risks of inbreeding (including mating among close relatives). In outbreeding species that typically have high genetic load, inbreeding depression is likely to be expressed. The risks of inbreeding depression are even greater in species that spread through vegetative reproduction because of the increased pollen supply from spatially clustered genetically identical ramets.

Tanoaks can produce large acorn crops and also reproduce prolifically by basal resprouts. The large heavy seeds are dispersed by gravity, or by birds and small mammals, so that seed dispersal distances are likely to be short (Scofield et al. 2010; Moran and Clark 2012). This, combined with the potential local accumulation of stems of resprout origin should result in fine-scale genetic structure composed of demes of related individuals. The spatial scale of clonality and of relatedness become important parameters in determining the minimum distances that should be observed in selecting trees for seed collection to minimize risks of increased inbreeding in re-vegetated sites.

Clonal Spread

Detection of members of a clone (ramets) requires molecular markers with sufficient power that a pair of individuals with identical genotypes can be confidently assigned to a clone and are unlikely to be of seed origin. Using a set of eight nuclear microsatellite markers, Dodd et al. (2013) reported an average of 1.6 ramets per tanoak genet in mature upland and lowland stands. A frequency histogram of numbers of ramets per genet shows large numbers of single-ramet genets and a maximum of five ramets per genet on lowland sites and eight ramets per genet on upland sites (Fig. 2a). The maximum spatial distance over which the ramets were distributed, estimated as the zero intercept of a logistic function fitted to a plot of frequency distributions of different distance classes (Fig. 2b) was 6.5 m on upland sites and 5.5 m on lowland sites. One problem with rapidly mutating markers such as nuclear microsatellites is ramets may not have identical genotypes because of somatic mutations (Ally et al. 2008). Therefore, if resprouting has been occurring over generations, different mutations could arise among the ramets and the estimates of ramet number and distance based on identical genotypes could be underestimated. Although Dodd et al. (2013) allowed for a single step mutation at their microsatellite loci for assignment of non-identical ramets to a genet lineage (multilocus lineages), this did not increase significantly the estimates of numbers and spread of ramets. Based on the single location for their study, clonal spread appears not to have exceeded about 6–7 m.

Spatial Genetic Structure

Fine-scale genetic structure for neutral genetic markers arises mainly as a result of the balance between gene dispersal and stochastic processes of genetic drift. Assuming a population to be in drift-dispersal equilibrium, genetic neighborhoods that define a circle within which parents

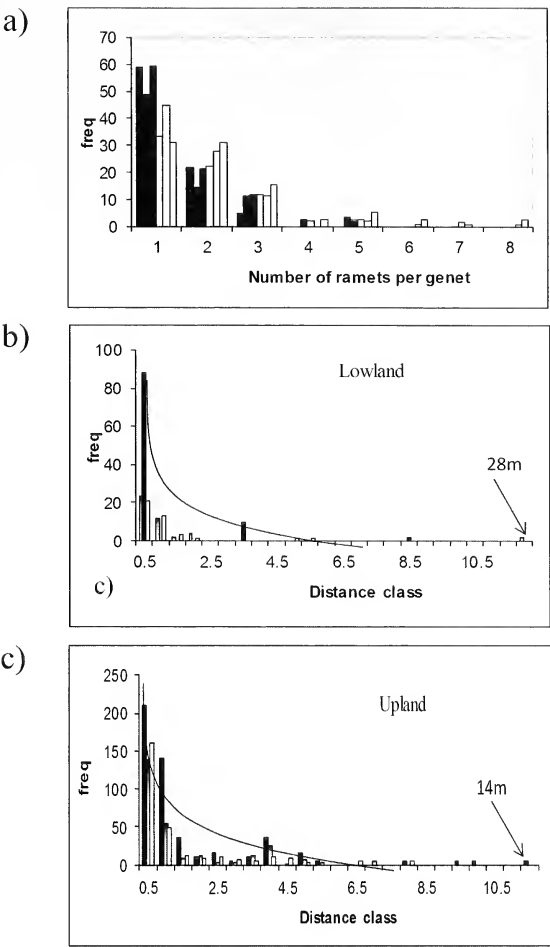


FIG. 2. (a) Frequency distribution of numbers of ramets per genet (solid bars: lowland sites and unfilled bars: upland sites); (b and c) frequency distributions for clone mates within distance classes for lowland and upland sites (three replicate sites shown as grey, solid and open bars. Fitted logarithmic function $y = -13.8 \ln(x) + 22.8$ for lowland site and $y = -39.9 \ln(x) + 74.5$ for upland site. Adapted from Dodd et al. (2013).

of most of the individuals reside, can be estimated using classical population genetic theory for models of continuous populations (Wright 1943). A two-dimensional neighborhood size ($N_b = 4\pi\sigma^2d$) is normally distributed with radius 2σ , where σ (standard deviation of dispersal) defines the displacement of progeny from parents, and d is the population density. Neighborhood size (N_b) can be inferred from spatial patterns of relatedness estimated from molecular data that allows inference of σ^2 (Vekemans and Hardy 2004) and effective plant density. Wright's model can be extended to include the composite effects of seed dispersal, pollen dispersal and vegetative spread (Gliddon et al. 1987). Dodd et al. (2013) estimated neighborhood sizes in tanoak as a function of clonal spread and of sexual dispersion. Clonal

spread averaged 1.7 m on lowland sites and 2.1 m on upland sites, whereas sexual dispersion averaged 69.3 m on lowland sites and 46 m on upland sites. These dispersal distances are evolutionary measures that make a number of assumptions, most importantly that populations are in equilibrium and that dispersal follows a normal distribution. Neither of these assumptions is realistic; populations need long periods of environmental stasis to reach equilibrium and dispersal distances are more likely to be leptokurtic with most progeny being close to parental individuals. Nevertheless, the estimates of dispersal distances from genetic neighborhoods provide the best indications of how far apart trees for seed collection should be to minimize relatedness, in the absence of direct estimates from progeny arrays (multiple seeds from a single parent) to infer parentage.

IMPLICATIONS FOR REPLANTING

Present indications are that the SOD pathogen will continue to cause epidemics resulting in severe mortality of tanoak trees and that the ecosystems in which tanoak is dominant are likely to be transformed, with tanoak being represented only in the understory as resprouts (Cobb et al. 2012). So far, ecological monitoring is insufficient to determine the long-term survival of resprouts, or whether some genotypes are likely to be more persistent than others as clones. Assuming continued mortality of adult trees, stands through which disease has spread will have smaller effective population sizes, as fewer individuals will reach seed-producing age. To augment the loss of tanoak, vegetation managers need guidelines for the selection of seed for replanting. Breed et al. (2011) describe a range of seed sourcing strategies aimed at minimizing the effects of inbreeding and outbreeding depression, avoiding or mitigating introduction of mal-adapted genotypes and providing a diverse genetic base for adaptation to environmental change. We examine these options for tanoak and recommend under what circumstances they may be appropriate and what further research is needed to optimize success of replanting.

Local Provenancing

Although the use of local seed sources is the most commonly adopted strategy, it is best reserved for a system in which only local populations exist (Breed et al. 2012). Under these conditions risks of outbreeding depression and introducing mal-adapted genotypes are minimized. For tanoak this may be important in peripheral populations such as the southern range where populations are more isolated (see discussion above) and in the interior coastal range where populations reach their distribution-

al limit. There are two major disadvantages of this approach. First, if populations are small, they may not be optimally adapted to their local environment because of genetic drift. This will be exacerbated by the selection of a relatively small seed pool for replanting. If adopted, seed should be selected from trees that are least likely to be related. Ideally, research is needed to determine dispersal distances of seed and pollen to determine minimum distances among seed trees for each population in need of replanting. If this is not possible, the minimum distances described above from the study at Jackson Demonstration State Forest can be applied. However, we know very little about pollen dispersal in this insect-pollinated species and factors affecting pollinators will play an important role in the size of genetic neighborhoods. The second disadvantage of local provenancing is that it does not account for environmental change. This is likely to be very important in the southern range of the species, including areas of high mortality levels in Monterey County.

Predictive Provenancing

This approach requires information on plant performance under a range of experimental conditions. This can be provided by reciprocal transplant studies, but these have not been performed for tanoak. The great advantage of this technique is that phenotypes can be identified that should perform well at the replanting site. Furthermore, climate modeling can provide some inferences on future climate at the site so that phenotypes can be selected that are expected to match future climates. Substantial work is needed before this approach can be implemented for tanoak. However, reciprocal transplant plots are a worthy investment to obtain valuable information on translocation success.

Composite Provenancing

The objective of this approach is to attempt to mimic landscape patterns of gene flow and to incorporate a mix of planting stock that reflects the probable pool of genotypes that would naturally contribute to the evolutionary potential of the site (Broadhurst et al. 2008). This requires knowledge of patterns of gene flow and differentiation at scales from 100s to 1000s of meters. This scale is intermediate between the species-scale and the fine-scale described above for tanoak. Advantages of this approach are that seed provenances can be detected that are tied together by gene flow and quantities of seed from the different sources can be selected so that the risk of genetic swamping and introduction of mal-adapted genotypes is low, and provenances can be selected that account for climate change.

Genetic data at this scale are not available for tanoak, but they could be obtained at relatively low cost.

Admixture Provenancing

Admixture provenancing (Breed et al. 2012) selects seed from different environmental conditions within large populations. Unlike composite provenancing, no account is taken of dispersal distances, but sampling can be skewed to favor seeds from sites whose climate is likely to match future climate at the replanting site. Although, this approach is likely to introduce maladapted genotypes, Breed et al. (2012) claim that these should rapidly be purged from the population, but this would require large numbers of seedlings and would introduce the risk of outbreeding depression in the next generation. Therefore, provenances taken at great distances from the replanting site should first be tested in crossing studies and reciprocal transplants. For tanoak, we highly recommend that this type of approach should not mix provenances from the five major groups (Santa Barbara, Lompoc, central and northern coastal California, extreme northern California and Oregon, interior populations from the Sierra Nevada) described under Genetic structure at the species level above.

CONCLUSIONS

Our knowledge of genetics of tanoak is still at an early stage, but it does provide some guidelines that will be important for future management of tanoak stands if SOD continues to cause high levels of mortality. Here we have reviewed some of the published work that addresses population processes and the implications for choice of seed sources for replanting after mortality from SOD. In this issue, Wright and Dodd provide evidence that tanoak is insect pollinated that contrasts with the pollination syndrome in the true oaks. This is likely to have implications for patterns of pollen dispersal that in turn will be influenced by environmental changes associated with the disease, with population fragmentation and with climate change. We still have much to learn about the ecological processes that affect genetic diversity in this species and the consequences for conservation and revegetation under the combined challenges of disease, development and climate change.

ACKNOWLEDGMENTS

This work was supported by the USDA Forest Service, Pacific Southwest Research Station (06-JV-11272138-047 and 06-JV-11272138-069 to R.S.D.).

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RANGE-WIDE THREATS TO A FOUNDATION TREE SPECIES FROM
DISTURBANCE INTERACTIONS

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ABSTRACT

The geographic range of tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), encompasses tremendous physiographic variability, diverse plant communities, and complex disturbance regimes (e.g., development, timber harvest, and wildfire) that now also include serious threats posed by the invasive forest pathogen *Phytophthora ramorum* S. Werres, A.W.A.M. de Cock. Knowing where these disturbance factors interact is critical for developing comprehensive strategies for conserving the abundance, structure, and function of at-risk tanoak communities. In this study, we present a rule-based spatial model of the range-wide threat to tanoak populations from four disturbance factors that were parameterized to encode their additive effects and two-way interactions. Within a GIS, we mapped threats posed by silvicultural activities; disease caused by *P. ramorum*; human development; and altered fire regimes across the geographic range of tanoak, and we integrated spatially coinciding disturbances to quantify and map the additive and interacting threats to tanoak. We classified the majority of tanoak's range at low risk (3.7 million ha) from disturbance interactions, with smaller areas at intermediate (222,795 ha), and high (10,905 ha) risk. Elevated risk levels resulted from the interaction of disease and silviculture factors over small extents in northern California and southwest Oregon that included parts of Hoopa and Yurok tribal lands. Our results illustrate tanoak populations at risk from these interacting disturbances based on one set of hypothesized relationships. The model can be extended to other species affected by these factors, used as a guide for future research, and is a point of departure for developing a comprehensive understanding of threats to tanoak populations. Identifying the geographic location of disturbance interactions and risks to foundation species such as tanoak is critical for prioritizing and targeting conservation treatments with limited resources.

Key Words: Decision support system, fire, forest ecosystems, foundation species, landscape epidemiology, *Notholithocarpus densiflorus*, sudden oak death, tree disease.

Ecological disturbance regimes play an integral role in ecosystem dynamics by altering resource availability, modifying ecosystem structures, and creating new landscape spatial patterns (e.g., Mou et al. 1993; Spies et al. 1994; Turner et al. 2003). Increasing global connectivity, population growth, and climate change are rapidly altering disturbance regimes, resulting in the emergence of novel disturbance interactions with pronounced impacts to socio-ecological systems from local to global scales (Turner 2010). Interacting disturbance regimes that alter the abundance and structure of foundation species effectively disrupt the fundamental ecosystem processes that they support and stabilize, such as clean water, decomposition, and carbon sequestration (Chapin et al. 1997; Ellison et al. 2005), which are vital for maintaining the physical, social, and economic health of human populations (Costanza et al. 1997). Recognition of the relationships and impacts of disturbance interactions by local, regional, and global stakeholders is necessary to

manage for the resiliency of foundation species and their functions (Folke et al. 2004). Research explicitly addressing the effects of interacting disturbances in forest ecosystems has recently increased (e.g., Bebi et al. 2003; Buma and Wessman 2011; Metz et al. 2011), but we still understand relatively little about their impacts. The landscape heterogeneity and spatial extent over which forest disturbances occur challenges the development of ecosystem conservation strategies, presenting a pressing need to develop tools that engage and guide stakeholders in achieving conservation objectives across these broad areas.

Accessibility to and familiarity with geographic information system (GIS) technologies (e.g., GPS-enabled smartphones and online mapping) has become more widespread in recent years, increasing the potential to effectively bring stakeholders together in addressing complex conservation management problems. Spatially explicit models developed using GIS can be

utilized as spatial decision support systems to identify the geographic location and potential severity of disturbance events, providing an essential tool for threat assessment and management. This adaptable framework can be applied to identify at-risk populations when the models are built using known biological relationships and sound ecological theory, even when knowledge of the precise relationships is scant. For example, Andersen et al. (2004) developed a risk model of threats to biodiversity across a large, heterogeneous landscape by examining relative risk of land use factors on several resident taxa, and Meentemeyer et al. (2004) similarly mapped the risk of establishment and spread of a forest pathogen (*Phytophthora ramorum* S. Werres, A.W.A.M. de Cock) across California. Mapping the threat to the abundance and structure of foundation species from disturbance interactions helps guide stakeholders in developing and implementing effective conservation strategies that protect vital ecosystem services.

Tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), is a foundation species threatened with functional extinction by multiple interacting disturbances throughout large portions of its range. This tree is, a dominant component of the ecosystems it inhabits (Cobb et al. this volume), has unique ecological characteristics in coastal California forests (Bergemann and Garbelotto 2006; Wright and Dodd this volume), and as the lone representative of its genus it is a significant contributor to regional as well as global biodiversity. This shade-tolerant tree can form multi-storied forest canopies with other dominant overstory species, providing important stand structure for wildlife, such as the spotted owl (*Strix occidentalis*; LaHaye et al. 1997; North et al. 1999). Tanoak acorns are a traditionally important nutrition source for Native Americans, and the trees were a principal source of bark-extracted tannins until the advent of chemical tanning compounds in the 1950's (Bowcutt 2011). Since the collapse of the tanoak bark market, perspective on this species has shifted from an important forest commodity to an impediment to production of more valuable timber species, such as redwood, *Sequoia sempervirens* (Lamb. ex D. Don) Endl., and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. Since the 1950's, most applied forest research on tanoak has focused on techniques to reduce competition with timber species, primarily through herbicide applications to reduce tanoak prevalence and biomass in forests managed for timber production (Harrington and Tappeiner 2009; Bowcutt 2011). In the last ten years, *Phytophthora ramorum*, and the resulting disease sudden oak death, has emerged as a major cause of tanoak mortality in central coastal California, and increasingly in northern

coastal California and southwest Oregon (Rizzo et al. 2005; Meentemeyer et al. 2008; Václavík et al. 2010). *Phytophthora ramorum* has a large array of hosts, but susceptibility, impacts of infection on host health, and the competency of hosts to transmit infection varies dramatically over the 137 regulated native and exotic host species (APHIS 2012).

Silviculture, disease, development, and altered fire regimes are arguably the major disturbances threatening the abundance, function, and persistence of tanoak throughout its range. Silvicultural practices have explicitly suppressed tanoak to promote the growth of conifer species; human population expansion has resulted in conversion of forested land to development; and fire regimes have been altered from historic baselines (Havlin et al. 2010). In addition to these disturbances, tanoak is being severely impacted by *P. ramorum* on local to regional scales (Meentemeyer et al. 2008; Meentemeyer et al. 2011; Cobb et al. 2012b). Tanoak readily supports sporulation of *P. ramorum* and can be rapidly killed following infection by this pathogen (Hansen et al. 2008). Several other common native species also support sporulation, but do not die following infection, most notably California bay laurel, *Umbellularia californica* (Hook. & Arn.) Nutt. (DiLeo et al. 2009). Thus, the distribution of bay laurel and tanoak strongly influences the risk of pathogen establishment and disease emergence (Meentemeyer et al. 2004; Davidson et al. 2008; Cobb et al. 2010). The geographic variation and extent of each of these disturbances present major challenges to the conservation of tanoak ecosystems.

We present a spatially explicit model to quantify and map the area threatened by these four disturbances and their interactions across the geographic range of tanoak. This hypothesis-based modeling approach is readily integrated with adaptive management strategies. Thus, as knowledge of the system grows, the parameters of our model can be adjusted in accordance with evolving goals and the efficacy of treatments.

GEOGRAPHIC RANGE

The geographic range of tanoak stretches contiguously along the Pacific coast from a four-county area in southwestern Oregon in the north, to Monterey County, CA, in the south, with disjunct populations occurring in the Sierra Nevada foothills to the east. Our analysis excluded an isolated population occurring near Santa Barbara, CA (Tappeiner et al. 1990), because the data we used for tanoak abundance and area estimates (Lamsal et al. 2011) were incomplete in this region. Tanoak's geographic range possesses tremendous physiographic variability and complex disturbance regimes, and is broadly characterized by a Mediterranean-type

TABLE 1. THE WEIGHTS ASSIGNED TO INDIVIDUAL DISTURBANCE FACTORS AND THE INTERACTIONS IN THE INITIAL MODEL BASED ON OUR INTERPRETATIONS OF RELEVANT LITERATURE AND EXPERT OBSERVATIONS. Each disturbance factor was first standardized to a 0–3 ranking so that assigned weights used in the modeling calculations reflect their relative importance as a threat to tanoak.

Disturbance	Weights
silviculture	30
disease	25
development	10
fire	5

Interaction	Interaction weight
disease x fire	2
disease x silviculture	2
disease x development	1
fire x development	1
development x silviculture	1
fire x silviculture	1

climate with cool, wet winters and warm, dry summers. Tanoak occurs from sea level to roughly 2190 m, with greater abundance in forests on the leeward side of the Coast Range (Lamsal et al. 2011).

MODEL DEVELOPMENT

We developed a rule-based spatial model to quantify and map the relative threat to tanoak populations from four disturbance factors occurring throughout tanoak’s geographic range. This heuristic approach is akin to a mental shortcut, where empirically undefined relationships can be hypothesized and examined. In order to parameterize the relative threat to tanoak from each disturbance factor, we classified the threat level of each factor at a particular location into an integer ranking system from zero to three, with zero representing no threat and three representing high threat. At each location, we assigned each factor a low (1), intermediate (2), or high (3) threat ranking by breaking the range of values greater than zero into three equal intervals. We also assigned a weight value to each ranked disturbance factor indicating its relative importance as a threat to tanoak (Table 1). We based these weight values on our interpretations of published research and expert knowledge evaluating the impacts of each disturbance to tanoak. They can be altered within the modeling framework to explore other hypotheses of the impacts to tanoak from these disturbances. We calculated multiplicative two-way disturbance interactions for each location, assigning an additional exponential term to weight the interaction that we hypothesized as representing the greatest threat to tanoak (Table 1). For each location, we then selected the highest-valued interaction for inclusion in the

final threat calculation to visualize and highlight areas with the most at-risk populations for the set of hypotheses (i.e., weights) being examined.

The equation used to calculate potential threat to tanoak from these disturbance factors is the sum of the products of each factor’s rank and importance weight, plus the highest valued interaction at each mapped location (grid cell):

$$P_j = \sum_i^n W_i R_{ij} + [W_i^a R_{ij}^a \times W_i^b R_{ij}^b]^y \tag{1}$$

where P is the calculated risk for a grid cell in the model output, W_i is the weight of the i th disturbance factor, R_{ij} is the rank value of the i th factor at location j , and y is the weight assigned to the interaction of two factors. The interaction weight (y) is determined by which pair of weighted factors, $W_i^a R_{ij}^a$ and $W_i^b R_{ij}^b$, occur together at a given location (Table 1). The superscripts of these parameters (a and b) ensure that a factor is never multiplied by itself. We developed maps of each disturbance factor and overlaid them with a tanoak abundance surface (Lamsal et al. 2011). We then applied the interaction model (Eq. 1) in a GIS environment to generate a map of at-risk tanoak populations from these interacting disturbances across the geographic range. We classified the model output into a 1–3 threat-level ranking by breaking the calculated values at equal intervals. Similar to the individual factors, we qualitatively labeled the threat levels as ‘Low’ (1), ‘Intermediate’ (2), and ‘High’ (3). The lack of zero values in the final map output demonstrates that at least one factor was present at every estimated tanoak location.

QUANTIFYING NUMBER OF TANOAK AT RISK

We quantified the area and number of tanoak trees in each threat category by intersecting the output of equation 1 with maps of tanoak density produced by Lamsal et al. (2011). These data were further organized by county to aid to regional decision making. We then multiplied the county-level tanoak areas (hectares) in each threat level by the average number of tanoak per hectare in each county derived from data provided by Lamsal et al. (2011). This produced the estimated number of tanoak in each threat category for each county in the study system. We report on a limited number of areas in this paper, with more detailed county summaries available from the authors.

DISTURBANCE FACTORS

Silviculture

Beginning in the early to mid-20th century, silviculture in Oregon and California strongly

avored softwood conifer species at the expense of hardwood species, especially tanoak (Bowcutt 2011). Most notable are broad-scale applications of herbicide to reduce tanoak competition with timber species in these forests. Tanoak vigorously sprouts following cutting and can reduce the growth of planted or naturally regenerating conifers (Harrington and Tappeiner 1997; Lorimer et al. 2009). Herbicide applications are effective in reducing tanoak cover and increasing the growth and dominance of coniferous timber species (Tappeiner et al. 1987; Harrington and Tappeiner 2009). When applied as a broadcast spray from aircraft, or at very high efficiencies by ground crews, it is reasonable to expect these practices would result in functional extinction of tanoak at local scales. For these reasons, the silviculture risk factor received a weight of 30, the highest weight (Table 1).

We developed the silviculture risk factor layer using Forest Inventory and Analysis (FIA) (USDA 2008) data for plots in California and Oregon where tanoak was reported ($n = 565$). FIA surveys record evidence of silvicultural treatments that affect areas of one acre or more; however, they do not specify herbicide application. We assumed the following about these data: 1. silviculture activities included suppression of undesirable species, i.e., tanoak, 2. a greater number of treatments is equivalent to greater threat to tanoak populations, and 3. recent treatments were more efficient and effective, whereas older treatments may have been overcome by recolonization from tanoak in adjacent stands (Tappeiner and McDonald 1984). We used all recorded treatment types with the exception of "Firewood or local use cut," which we interpreted as unlikely to target tanoak (or any species) for removal or suppression. We ranked locations according to the number of recorded treatments weighted by the timing of those treatments. We used 20-year intervals to capture increased activity surrounding timber harvests as well as related treatments during intervening years. This process assigned the highest risk from silviculture to locations where treatments were both persistent and more recent. We used these scores to create a map of silviculture intensity with values ranging from 0–10, which we reclassified into 0–3 rankings by splitting non-zero values at equal intervals.

Disease

Phytophthora ramorum is an unprecedented pathogen in terms of its capacity to impact the abundance, structure, and function of tanoak communities. The mortality rate of *P. ramorum* infected trees (especially tanoak but also *Quercus* species) increases with tree size (Ramage et al. 2011; Cobb et al. 2012b), leading to rapid declines

in tanoak biomass, dominance, and ecological function. We assigned the disease factor a weight of 25, slightly lower than silviculture because its impact on tanoak is slower, more heterogeneous, and highly dependent on other landscape and vegetation characteristics (Haas et al. 2011). For the disease disturbance factor, we used two previously developed maps detailing the risk of *P. ramorum* establishment and spread for Oregon (Václavík et al. 2010) and California (Meentemeyer et al. 2004). These studies used heuristic models incorporating host indices and climate factors derived from known infestations to characterize disease risk throughout each landscape. We created a mosaic of these independent risk layers with values ranging from 0–100, and reclassified this map along equal intervals into 0–3 rankings.

Development

Development impacts tanoak abundance, function, and persistence through conversion of forests to developed landscapes characterized by mixtures of impervious surfaces, soil, and vegetation (including forest remnants, planted lawns, shrubs, and trees). In addition to this direct impact, development also increases human activity in extant wildland areas. We interpreted the direct threat to tanoak from development to be relatively less than from disease and silviculture factors, but greater than from fire and assigned it a weight of 10 (Table 1). To estimate tanoak area at risk from development, we produced a development density layer for the geographic range using 2006 data from the National Land Cover Database (NLCD) (Fry et al. 2011).

The NLCD classification system breaks its level 1 "Developed" class into four sub-categories based on a ratio of human-made impervious surfaces to vegetation present within $30 \text{ m} \times 30 \text{ m}$ pixels as mapped from Landsat Enhanced Thematic Mapper (ETM+) imagery. Thus, as the relative proportion of impervious surfaces increases, the development "intensity" increases from a "developed low intensity" to "developed high intensity" category. We reclassified the NLCD low to high development intensity categories into our ranking system so that one, two, and three represented low, moderate, and high respectively, with the assumption that higher development intensity presents a greater threat to tanoak. We reclassified all remaining undeveloped NLCD classes to zero. We resampled this layer to $100 \text{ m} \times 100 \text{ m}$ cells to match the smallest grain size of other spatial data being utilized. We then generated a development density surface by summing all rank values (0–3) within a 500 m radius (i.e., $1 \text{ km} \times 1 \text{ km}$ rectangular neighborhood) of each grid cell location. This process effectively spreads some

development risk into adjacent undeveloped areas. We then reclassified the resulting development density map (values ranging from 0–75) into our common 0–3 ranking system using equal intervals.

Fire

Tanoak is a species well adapted to survive and recover from fire. Mature trees have thick, fire resistant bark, and it vigorously regenerates from basal sprouts following mortality of the above ground portion of the tree (Tappeiner et al. 1990). These characteristics enable tanoak to persist and often thrive in a wide range of fire regimes, including areas of low fire frequency (Hunter 1997), albeit with varying functional roles. We hypothesized that fire regimes altered from historic baselines as well as increases in potential fire severity from higher fuel loads result in greater threat to tanoak populations. Thus, we developed the fire disturbance factor to incorporate departure from historic fire regimes and potential fire severity. We represented departure from historic fire regimes using Fire Regime and Condition Class (FRCC) layers created for Oregon (USDA 2010) and California (CDF 2003). FRCC is an interagency, standardized tool for determining the degree of departure from reference condition vegetation, fuels, and disturbance regimes (Havlina et al. 2010). FRCC layers consist of ranked categories that quantify the difference between current vegetation conditions and fire frequency from historic reference conditions. Three ordinal categories rank the degree of departure from reference conditions in addition to a ‘not applicable’ category based on land cover type. We represented potential fire severity using fuel risk layers developed for Oregon (ODF 2006) and California (CDF 2005). The fuel risk layers were similarly categorized with three ordinal rankings of fuel risk and one indicating ‘not applicable’ due to land cover type. We recoded these existing categories of the fire regime departure and fuel risk layers to the 0–3 ranking scheme. We then summed the two layers and reclassified the resulting values (ranging from 0–6) to the 0–3 rankings. Given tanoak adaptations to fire and its occurrence and persistence under a variety of fire regimes, we assigned the fire factor the lowest weight of 5 (Table 1).

DISTURBANCE INTERACTIONS

We calculated two-way multiplicative interactions for all possible disturbance pairs at a given location weighted by the assigned exponent (y , Eq. 1). In locations where more than two factors overlapped, we selected only the highest-ranking interaction for calculating the threat value at that location. Using this approach, we assumed that

one set of disturbance interactions is the dominant threat to tanoak at a given location for the set of hypotheses (i.e., factor and interaction weights) being examined. Below, we describe our reasoning behind the weights assigned to each interaction parameter in our initial model (Table 1).

Disease x Fire

We assigned the disease-fire interaction a weight of two, reflecting our hypothesis that the threat to tanoak increases where these factors coincide. Importantly, *P. ramorum* has been shown to decrease average tanoak size (Davis et al. 2010; Cobb et al. 2012b), and tree size is closely associated with the likelihood of post-fire tree survival (Hengst and Dawson 1994; Kobziar et al. 2006). This disease also increases fuel loads (Valachovic et al. 2011; Cobb et al. 2012a), which are associated with increased soil damage following fire (Metz et al. 2011). Thus, we hypothesize that tanoak in disease-impacted areas are more susceptible to fire-caused mortality, and that dead material from disease would increase fire severity (particularly ground fire), further impacting tanoak recovery. Notably, slower or reduced tanoak recovery would decrease sources of *P. ramorum* inoculum.

Disease x Silviculture

We assigned the interaction of disease and silviculture factors a weight of two. This hypothesis is supported by research demonstrating the effectiveness of herbicide applications in causing tanoak mortality and reducing tanoak dominance (Tappeiner et al. 1987; Harrington and Tappeiner 2009), and the broad patterns of tanoak mortality (Meentemeyer et al. 2008) and reduced average tree size in disease impacted forests (Cobb et al. 2012b). In stands where these disturbances coincide, they have the potential to permanently remove large, mature tanoak trees. More broadly, actions such as salvage harvesting can increase the decline of dominant tree species already impacted by landscape level outbreaks of insects or pathogens (Kizlinski et al. 2002; Foster and Orwig 2006; Freinkel 2007). Tanoak generally has little or a restricted specialty market value, and so salvage harvesting is unlikely to occur for this species. However, herbicide use has a similar effect on tanoak populations except that it may be more efficient in reducing tanoak biomass (Tappeiner and McDonald 1984). Forestry practices may also decrease local tanoak populations to levels where *P. ramorum* is unable to invade stands, but these stands would likely be devoid of ecological functions unique to tanoak (Cobb et al. 2012b; Wright and Dodd this volume).

Development x Fire

This term aims to characterize the threat to tanoak from increased fire frequency related to development density. Syphard et al. (2007) showed that fire incidence is greatest at the wildland-urban interface; however, we did not have explicit evidence for this relationship within the geographic range of tanoak. It is also likely that these fires would be aggressively combated resulting in smaller fires with shorter burn times compared to more remote areas. Thus, we assigned the interaction of these factors a weight of one (Table 1).

Development x Disease

This term represents risk to tanoak based on the relationship between higher development density and increasing likelihood of disease introduction events. While development alone has no direct physical impact in this case, Cushman and Meentemeyer (2008) showed an increased probability of *P. ramorum* occurrence in forests near higher population densities, suggesting that roads, larger populations, urban and suburban landscaping, and heavier use of wildland recreation areas provide additional spatial pathways for pathogen movement and introductions. However, we did not interpret this relationship as producing a significant impact relative to other interactions and so assigned it a weight of one.

Development x Silviculture

Silviculture and development require infrastructure (e.g., roads) for transportation and accessibility. This infrastructure enables further silviculture, recreation, and development activities. We hypothesized that this interaction would nominally increase the threat to tanoak and so assigned it a weight of one.

Fire x Silviculture

While silviculture reduces average tree size and therefore predisposes individual stems to fire-caused mortality, we also hypothesize that it reduces the risk of wildfire ignition and may reduce potential severity. Additionally, tanoak adaptations producing robust sprouting and growth following fire or timber harvest allow for an increased likelihood of tanoak persistence when these factors interact, though most mature trees may be removed. According to these postulations, we assigned this interaction a weight of one.

SENSITIVITY ANALYSIS

We tested model sensitivity to interaction parameters by varying interaction weights in a series of model runs. We ran the model with all

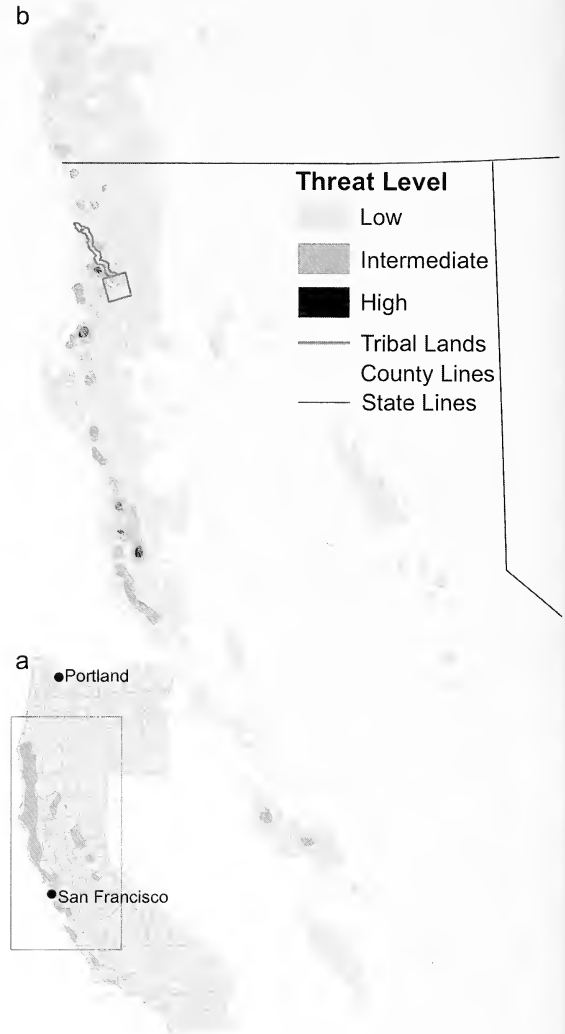


FIG. 1. The spatial distribution of (a) tanoak and (b) threats from weighted interacting disturbances (see Table 1) across tanoak's geographic range. Tanoak range adapted from Tappeiner (1990). Tanoak populations facing elevated threats were concentrated in Humboldt and Mendocino Counties, and partially located on Hoopa and Yurok tribal lands.

interaction weights set to zero, which produced threat values for only the additive part of the model. While this sums the weighted rank values occurring at each location it does not provide insight into local factor interactions. We then ran the model with all the interaction weights set to one (equally weighted) and used multiple iterations to examine how results changed when each interaction term was assigned a weight of two while holding all other factors at one. These tests produced no zero values, indicating that at least one factor was present at each location in our map of tanoak distribution (Lamsal et al. 2011). Using equal intervals, we reclassified the resulting



FIG. 2. Four disturbance factors overlaid on estimated tanoak area. Each map shows the classified threat level to tanoak from each disturbance factor across tanoak's geographic range, ranked zero to three ('none', 'low', 'intermediate', and 'high', respectively).

range of values from each model run into low (1), intermediate (2), and high (3) threat levels.

RESULTS

Risk from Disturbance Interactions

Across its geographic range tanoak predominantly faces low to intermediate threats from disturbance interactions, with smaller areas at high risk. The weights listed in Table 1 resulted in a threat map (Fig. 1) with 10,905 hectares (<1%) of estimated tanoak area at high risk, 222,795 ha (5.6% of estimated tanoak area) at intermediate risk, and over 3.7 million ha (94% of estimated tanoak area) at low risk from disturbance interactions. Elevated fire and silviculture risk factors overlap in the Sierra Nevada, whereas disease risk was low throughout much of this region (Fig. 2a, b, d). The influence of development on disturbance interaction risk was observed

primarily in the San Francisco Bay Area, where it coincided with low values for other disturbance factors (Fig. 2c). Tanoak faces intermediate and/or high threats from disturbance interactions in 20 of the 30 counties within its geographic range. Using this model formulation, areas classified as intermediate and high threat occurred predominantly where disease and silviculture factors overlapped (Figs. 1 and 2a, 2b). The intermediate and high categories covered 233,700 ha containing an estimated 134.4 million tanoak, with 108.9 million (81%) of these trees located in Humboldt and Mendocino counties, CA. Some of the elevated threat categories are located in areas where tanoak has high cultural importance, including on Hoopa and Yurok tribal lands (Fig. 1).

Sensitivity analysis of the interaction weights demonstrated general robustness of the total amount of tanoak area classified into low and intermediate threat levels, with these two categories accounting for 91% to 99% of the total tanoak range across model runs with different interaction weights. With interaction weights all held at zero (the sum of weighted factors only), nine percent of tanoak area was at high risk, 73% at intermediate risk, and 18% at low risk. With all interaction weights set to one (the sum of the weighted factors plus the highest valued interaction at each location), six percent of tanoak area was at high risk, 24% at intermediate risk, and 70% at low risk. Results from these analyses, respectively, highlight areas where overlapping disturbance factors accumulate and where higher weighted factors coincide. In sensitivity analyses with each interaction weight increased to two while holding others constant at one, we found the disease-silviculture interaction produced the same result as the weighting scheme of the initial model (Table 1). The fire-silviculture interaction resulted in values similar to those produced by our initial model parameters: 6419 ha (<1%) at high risk, 222,790 ha (5.6%) at intermediate risk, and 3.7 million ha (94%) at low risk. Most significantly, the disease-fire interaction was most sensitive to changes in the interaction weight parameter and resulted in five percent of tanoak area at high risk, 31% at intermediate risk, and 64% at low risk. Development impacts on risk were generally small and consistently resulted in >99% of tanoak area in the low threat category. Of the three disturbance interactions that included development, the disease-development interaction resulted in the greatest area in intermediate (9990 ha) and high (1593 ha) threat levels.

DISCUSSION

Mapping the geographic distribution of disturbance factors that threaten foundation species is essential for understanding and managing popu-

lation and ecosystem impacts (Holdenreider et al. 2004; Ellison et al. 2005). Since many landscapes are influenced by multiple disturbances, spatially explicit tools identifying areas at risk from disturbance interactions are critical to conservation of threatened populations. These tools can be used for prioritizing limited resources for efficient and effective conservation of at-risk species.

Since European settlement, harvesting of tanoak bark, and the subsequent increasing application of herbicides by industrial forestry interests to favor more marketable conifer species (Bowcutt 2011), undoubtedly altered the structure and function of tanoak forests. Coinciding with these processes was an increasing human population resulting in development of forest and wildlands, and alteration of fire regimes to favor conifer species that were valued over tanoak in post-1950 timber markets. Remarkably, tanoak has shown substantial resilience under these adverse conditions, but the introduction of *P. ramorum* into tanoak ecosystems presents a new and significant threat to this species. Although diseases can increase extinction risk (Smith et al. 2006), it is unlikely that tanoak could be eliminated by this pathogen alone. Species extinction most often occurs when multiple stressors coincide to reduce at-risk populations to unsustainable levels (de Castro and Bolker 2005; Smith et al. 2006). Analogously, disturbance interactions, especially novel ones such as those resulting from impacts of an emergent pathogen like *P. ramorum* (e.g., Metz et al. 2011), may increase the likelihood of stand-level tanoak extirpation. Thus, the functional extinction of tanoak due to the removal of all or most large trees over broad areas may be more likely to occur where disturbances interact (cf., American chestnut blight, Paillet 2002; jarrah dieback, Podger 1972).

Cobb et al. (2012b, this volume) indicated that significantly more *P. ramorum*-caused tanoak mortality is likely to occur over the coming decades. This is largely due to the epidemiological role of tanoak in driving pathogen spread and disease emergence, and the high abundance of tanoak in climates favorable to *P. ramorum* (Meentemeyer et al. 2011). Annual variability of temperature and precipitation significantly impact the likelihood of pathogen establishment and spread (Rizzo et al. 2005; Davidson et al. 2011), which was reflected in the observed difference in risk of disease establishment between coastal and inland landscapes (Fig. 2b; Meentemeyer et al. 2004; Václavík et al. 2010).

Global to regional climatic changes are forecasted to influence fire incidence, and changes in fire frequency and intensity could affect tanoak resilience. Moritz et al. (2012) projected significant increases of fire frequency in the near future

across much of the globe, including the west coast of North America. A significant portion of tanoak's geographic range coincided with intermediate and high threat categories for the fire factor in our analysis, emphasizing the threat to tanoak from altered fire regimes and increased fuel loads (Fig. 2d). The forecasted changes to fire regimes throughout tanoak's geographic range would increase the probability of interactions with other disturbances and consequently the threat to tanoak populations.

With this model, we identified locations where interacting disturbances have the potential to threaten tanoak populations. Knowing the geographic variation of disturbance interactions is fundamental for developing and implementing management strategies that are landscape appropriate. Managers and researchers can often identify the dominant disturbance influencing a landscape, but these events do not occur in a vacuum and individual disturbances can shape the nature and intensity of other events (Turner 2010). This model provides the capacity to identify, target, and test management treatments in the context of multiple disturbances and their interactions. For example, areas at high risk from interactions of silviculture and disease factors in Mendocino and Humboldt counties could be reduced through judicious use of "slow-the-spread" actions such as proactive thinning of smaller tanoak and California bay laurel. Meanwhile, maintaining tanoak contribution to ecosystem function in the face of silviculture could be accomplished by retaining large tanoak in stands managed for timber. Tanoak in the Sierra Nevada is primarily threatened by fire and silviculture interactions, again suggesting that retention of large tanoak in stands managed for timber would be appropriate to enhance habitat as well as maintain tanoak resilience to fire.

Using models to guide decision-making requires recognition of model assumptions and limitations, principally that results (in this case mapped disturbance interaction threats to tanoak) are often sensitive to the values of the input parameters. The weighting of disturbances and the interactions using the initial model parameters (Table 1) resulted in a map where the interaction of silviculture and disease factors produced intermediate and high threat levels to tanoak over a relatively small portion of tanoak's geographic range (Fig. 1). This essentially shows that high intensity silviculture and disease factors are concentrated in a few smaller areas. Also, these two factors could potentially be the most addressable by management action and minor alteration to forestry practices in these areas. Our sensitivity analysis demonstrated that the model is robust with respect to parameter values for disease and fire interactions. Further, these factors resulted in the greatest total tanoak area

at intermediate and high threat levels (>1.4 million ha, or 36%). This is indicative of the role of tanoak as a host of *P. ramorum* as well as the potential alteration to fire regimes in tanoak ecosystems following the establishment of *P. ramorum*. We emphasize that the results of our model represent threats based on hypothesized relationships among these disturbances. Field measurements are necessary to validate these expected outcomes and provide appropriate model updates for further predictions, such as actual measurements of tanoak mortality from each factor across a wide range of environments.

Apposite model interpretation is especially important when results are used to inform management actions, because misconception of either inputs or outcomes could lead to decisions that are contrary to stakeholder objectives. Through careful analysis, diverse management goals may be accomplished by applying more effective, or “designer” treatments to areas with distinct threats. For example, forests at low risk and currently unaffected by disturbances may be most appropriate for the establishment of refuge tanoak populations. Areas facing intermediate threat levels that also border regions with higher threat levels (Fig. 1) may be ideal for treatments that slow pathogen invasion into adjacent stands. The effective threat from interacting disturbances is temporally implicit, and the actual impacts to tanoak are dependent on the state of a stand, as well as the order and timing of disturbance events (Lorimer et al. 2009; Turner 2010). Therefore, the timing of treatments is an essential consideration. For example, fuel load reduction activities could also address disease risk by reducing densities of bay laurel and tanoak, but these treatments would be most beneficial when applied between July and the onset of winter rains to avoid introduction or spread of the *P. ramorum* pathogen (Davidson et al. 2008, 2011). Also regarding disease, management efficacy decreases with time since *P. ramorum* arrival (Filipe et al. 2012), highlighting the importance of treatments that may prevent establishment as well as rapid responses to new invasions in order to mitigate impacts (Meentemeyer et al. 2012). These actions can provide time and space needed to implement further treatments that reduce the cost of disease (and potential interactions with other disturbances) to local communities (Kovacs et al. 2011; Cobb et al. this volume). Lastly, policy changes favoring retention of high value tanoak habitat, especially in locations at high risk from disturbance interactions could be effective at reducing the rate and extent of tanoak population decline as well as maintaining biodiversity and ecosystem function.

Although the maps of areas at-risk from disturbance interactions are static, the databases used to produce them are typically dynamic as

new data is acquired and analyzed over time. As new discoveries are made and our knowledge of disturbance interactions and their impacts evolves, model parameters can be updated and results tested in order to maintain reliability of recommendations. Through integration into an adaptive management framework, updates can be quickly applied, enabling new strategies to be developed and implemented in a timely and effective manner. The model framework may also be similarly applied to examine the spatial variation of threats to other species from disturbance interactions.

CONCLUSIONS

With increasingly limited resources it is important to rapidly identify target areas where management actions will have the greatest chance of achieving objectives. We propose that this model of threats to tanoak from interacting disturbances could be used as part of an adaptive management plan to bring stakeholders together in prioritizing and achieving conservation of the abundance, structure, and function of tanoak trees and ecosystems. Tanoak is by all accounts a resilient species, persisting and sometimes thriving under a variety of pressures. By applying knowledge and tools currently available, this resiliency can be enhanced, tanoak mortality may be reduced, and the vital services provided by tanoak ecosystems can be conserved for the health and prosperity of current and future generations.

ACKNOWLEDGMENTS

We are grateful to Monica Dorning and four anonymous reviewers for helpful comments on previous versions of this manuscript. This research was supported by a grant from the National Science Foundation (EF-0622770) as part of the joint NSF-NIH Ecology of Infectious Diseases program, the Gordon and Betty Moore Foundation, and the USDA Forest Service, Pacific Southwest Research Station.

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BIODIVERSITY CONSERVATION IN THE FACE OF DRAMATIC FOREST
DISEASE: AN INTEGRATED CONSERVATION STRATEGY FOR TANOAK
(*NOTHOLITHOCARPUS DENSIFLORUS*) THREATENED BY SUDDEN
OAK DEATH

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ABSTRACT

Non-native diseases of dominant tree species have diminished North American forest biodiversity, structure, and ecosystem function over the last 150 years. Since the mid-1990s, coastal California forests have suffered extensive decline of the endemic overstory tree tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae), following the emergence of the exotic pathogen *Phytophthora ramorum* and the resulting disease sudden oak death. There are two central challenges to protecting tanoak: 1) the pathogen *P. ramorum* has multiple pathways of spread and is thus very difficult to eradicate, and 2) the low economic valuation of tanoak obscures the cultural and ecological importance of this species. However, both modeling and field studies have shown that pathogen-centric management and host-centric preventative treatments are effective methods to reduce rates of spread, local pathogen prevalence, and to increase protection of individual trees. These management strategies are not mutually exclusive, but we lack precise understanding of the timing and extent to apply each strategy in order to minimize disease and the subsequent accumulation of fuels, loss of obligate flora and fauna, or destruction of culturally important stands. Recent work identifying heritable disease resistance traits, ameliorative treatments that reduce pathogen populations, and silvicultural treatments that shift stand composition hold promise for increasing the resiliency of tanoak populations. We suggest distinct strategies for pathogen invaded and uninvaded areas, place these in the context of local management goals, and suggest a management strategy and associated research priorities to retain the biodiversity and cultural values associated with tanoak.

Key Words: California Floristic Province, disease ecology, genetic diversity, pathogen-caused extinction, pathogen management, *Phytophthora ramorum*, restoration, tanoak population decline.

To the detriment of cultural, economic, and silvicultural interests, North America has experienced multiple declines of dominant tree species following the introduction and spread of exotic pathogens, many of which are innocuous microbes or weak pathogens in their native ranges (Loo 2009). The quarantine of known pathogens and other techniques to avoid introduction of pathogens into novel environments are important actions to reduce pathogen spread on international and inter-continental scales (Brasier 2008). However, the host range, invasion history, and persistence in the environment of many forest pathogens suggest these invasive organisms have, or will become, naturalized in their new ranges. This challenging natural resource problem demands well-crafted management efforts to avoid the most extensive or severe impacts of forest pathogens.

The pathogen *Phytophthora ramorum* S. Werres, A.W.A.M. de Cock (Werres et al. 2001) exemplifies the destructiveness, epidemiological complexity, and difficulty in managing the most problematic invasive microorganisms (de Castro and Bolker 2005; Smith et al. 2006). *Phytophthora ramorum* was first introduced into California and spread into wildlands via infected nursery stock in Santa Cruz and Marin Counties from a yet unknown native range (Garbelotto and Hayden 2012; Grünwald et al. 2012). The pathogen subsequently spread to Big Sur (Monterey County) and Humboldt County, probably on infected plants, and has since become established in central-California coastal forests. Establishment of *P. ramorum* has been rapid during the ~20 years since its arrival; spread of the pathogen is aerial with extensive local dispersal (20–50 m) and less frequent but consistent long-distance events of 1–3 km (Hansen et al. 2008; Meentemeyer et al. 2008a; Garbelotto and Hayden 2012). *Phytophthora ramorum* causes the disease sudden oak death (Rizzo et al. 2002) which has been responsible for a regional-scale population decline of tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh (Fagaceae); formerly *Lithocarpus densiflorus* (Manos et al. 2008), as well as the mortality of hundreds of thousands of oak trees (*Quercus* spp.) from the red oak clade, primarily coast live oak (*Q. agrifolia* Née) throughout the invaded areas of California (Meentemeyer et al. 2008b; Davis et al. 2010; Metz et al. 2012).

Phytophthora ramorum has a broad host range, with over 140 known native and non-native plants including many trees, shrubs, forbs, grasses, and ferns common to the California floristic province (Grünwald et al. 2012). In California, sporulation occurs on multiple hosts, the most important of which is the common forest tree California bay laurel (*Umbellularia californica*, Hook. and Arn.). Sporulation also

occurs on tanoak twig lesions at levels sufficient to spread the pathogen as well as cause bole lesions which are the principal infections that lead to mortality in tanoak and oak. In California forests, sporulation can be an order of magnitude greater on bay laurel and peak amounts for both species occur during warm spring rain events (Davidson et al. 2005, 2008; Mascheretti et al. 2008). In California, both tanoak and bay laurel are central to pathogen spread within stands and across landscapes although risk of pathogen establishment and spread rates are more strongly affected by bay laurel density (Meentemeyer et al. 2008a; Davidson et al. 2011). Host impacts are strikingly different across species: *P. ramorum* infection often leads to tanoak mortality, but has no known deleterious impacts on bay laurel at either the individual or the population level (DiLeo et al. 2009; Cobb et al. 2010). In California, the stand-level densities of tanoak and bay laurel greatly influence tanoak mortality rate and population decline (Cobb et al. 2012b). Pathogen dynamics are somewhat different in Oregon forests where sporulation occurs year-round and bay laurel does not play a significant role in spread at the landscape scale (Hansen et al. 2008). However, in both Oregon and California forests, tanoak population decline is expected across much of its endemic range (Fig. 1; Meentemeyer et al. 2004; Václavík et al. 2010; Lamsal et al. 2011; Meentemeyer et al. 2011; Dillon et al. this volume).

Independent studies using repeated measurements of individual tanoak show that mortality rate of infected trees increases with size (McPherson et al. 2010; Cobb et al. 2012b). Although the mechanism for this increase is not known, the pathogen's selective removal of large tanoak leads to rapid, stand-level loss of tanoak biomass in *P. ramorum* invaded stands (Ramage et al. 2011; Cobb et al. 2012b; Metz et al. 2012). Basic biodiversity information such as acorn production rates, knowledge of species obligate to tanoak, and other ecological functions provisioned by mature tanoak trees have not been reported in the peer-reviewed literature. However, ecological functions of individual trees often increase with tree biomass, which scales exponentially with tree size (Lamsal et al. 2011; Cobb et al. 2012a). Selective removal of large trees is likely to accelerate loss of ecosystem characteristics directly associated with tanoak, such as ectomycorrhizal associations or provisioning of habitat for other native flora and fauna which rely on or are obligate to tanoak (Rizzo et al. 2005; Bergemann and Garbelotto 2006; Cobb et al. 2012b; Wright and Dodd this volume).

The distribution of tanoak varies across the landscapes of the California floristic province (Fig. 1), increasing in prevalence with latitude up to the northern range limit of the species in

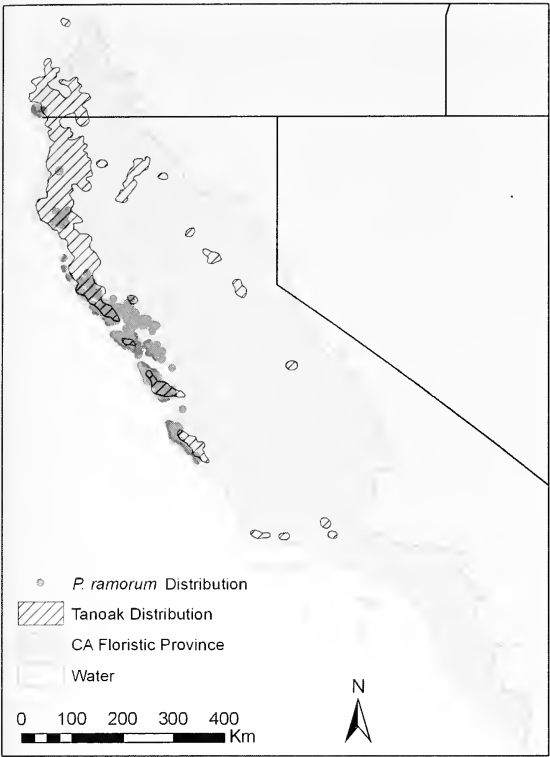


FIG. 1. The California floristic province with approximate extent of *P. ramorum* invasion and tanoak distribution. *Phytophthora ramorum* points are confirmed infected trees; the map was generated with publically available data accessed in January 25, 2013 from oakmapper.org and suddenoakdeath.org.

southwestern Oregon. Several notable disjunct populations are located in the northern Sierra Nevada foothills and in small, isolated populations in Santa Barbara County, CA (Fig. 1; Lamsal et al. 2011; Meentemeyer et al. 2011; Dillon et al. this volume). While *P. ramorum* establishment and disease emergence have been extensive in central coastal California, *P. ramorum* has not yet invaded the majority of the tanoak range (Meentemeyer et al. 2011). However, the pathogen is expected to invade culturally important, highly susceptible North Coast forests over the next several decades reflecting the opportunity and importance of planning and employing a proactive strategy to reduce disease impacts.

Phytophthora ramorum populations in newly invaded areas are often below thresholds where the pathogen can be detected using landscape-scale surveys. These cryptic invasions play an important role in landscape-level spread, and represent a critical challenge to eradication attempts and other pathogen-centric disease management strategies (Filipe et al. 2012). For many invasive pathogens, rapid responses that

match the scale of the outbreak increase the likelihood of successful eradication or the efficacy of slowing pathogen spread (Gilligan and van den Bosch 2008; Filipe et al. 2012). This requires rigorous study to identify effective management actions and minimize unintended impacts that are counter to the overall goal. Our intent here is not to review individual management techniques and their efficacy, rather we seek to bring together different management actions and place them in the context of local disease conditions and management goals. We begin by highlighting several historical and contemporary mistakes in forest disease management and emphasize the importance of incorporating historical lessons into sudden oak death management. We suggest how judicious use of established techniques can alter disease conditions and increase tanoak population resiliency across different forest types and community assemblages. We use the term ‘resiliency’ to mean retention of tanoak and the ecological functions provisioned by this tree and recognize that specific management objectives will vary among ownerships, agencies and situations. Part of our goal is to aid in the selection of when, where, and how to increase tanoak resiliency with existing management actions. We stress that management resources, land-owner cooperation, and chemical treatments will often be insufficient to control pathogen spread and disease emergence. Rather, when management actions aim to retain tanoak as a component of forest structure and composition, we advocate for integration of host-centric actions into management strategies. These strategies rely on increasing tanoak resiliency through stand manipulation to reduce sporulation, increasing distance among tanoak to reduce the probability of transmission, and identification of resistance in tanoak populations. Lastly, we stress that continuous feedback among sudden oak death research, management, and pathogen monitoring is needed to maintain tanoak as a component of biodiversity in many forests and to reduce the spread of *P. ramorum*.

LEARNING FROM FAILURE

The consequences of invasion of *Cryphonectria parasitica* (Murrill) Barr and the resulting disease, chestnut blight, is a notorious example of disease causing North American overstory tree loss (Anagnostakis 1987). Experience with chestnut blight can inform present-day challenges posed by exotic pathogens, especially *P. ramorum*. *Cryphonectria parasitica* is a generalist pathogen, selectively removes American chestnut (*Castanea dentata* Marsh.) from forest stands, and readily disperses across local and regional scales (Loo 2009). Within 30 years of introduction by the pathogen, these characteristics caused a widespread

decline of American chestnut and loss of the considerable ecological, cultural, and economic value that was associated with this species (Anagnostakis 1987; Freinkel 2007). The rate and extent of chestnut decline was unprecedented when the disease emerged circa 1900, and remains as one of the most infamous diseases in North American forest history because of the significant economic and cultural impacts caused by the epidemic (Freinkel 2007).

Chestnut blight is also notable as a case of failed management that stemmed from decisions with incomplete knowledge of pathogen biology and host relationships. For example, the state of Pennsylvania initiated an ambitious plan to remove infected chestnut trees and create a barrier zone with the intention of restricting pathogen spread into the western portion of the state (Freinkel 2007). However, understanding of *C. parasitica* transmission pathways, estimates of pathogen spread rate, and the capacity to detect cryptic infection were all inadequate and pathogen spread was unabated. A consequence of dedicated and extensive chestnut cutting was, at a minimum, an acceleration of chestnut removal from the overstory of these forests, an action that may have even expedited pathogen spread (Freinkel 2007). Today, American chestnut remains common in eastern forests as an understory shrub, but overstory trees and their associated ecological functions such as provisioning of large, nutritious, low-tannin nuts, have been lost from most of the species' former range (Paillet 2002). A full accounting of changes to native flora and fauna is hampered by the lack of natural history investigations of species associated with the tree prior to the epidemic. Although other species replaced American chestnut in the overstory, loss of chestnut probably impacted small mammal and invertebrate populations and may have resulted in the extinction of several insects obligate to this overstory tree (Orwig 2002; Ellison et al. 2005).

Regrettably, chestnut blight is not the sole example of misdirected or ineffective management actions. Eastern hemlock (*Tsuga canadensis* L.) forests are in decline across its native range from Georgia to southern Vermont and New Hampshire due to the invasion and subsequent regional-scale outbreak of hemlock woolly adelgid (*Adelges tsugae* Annand), an exotic insect pest (Fitzpatrick et al. 2012; Orwig et al. 2012). Eastern hemlock decline has been accelerated in southern New England by pre-emptive hemlock harvesting, regardless of stand invasion status (Orwig et al. 2002). From a conservation perspective, indiscriminant host tree removal will accelerate population declines of trees threatened by insect or disease outbreak as well as degrade the genetic diversity of remaining populations (Foster and Orwig 2006; Broadhurst et al. 2008).

Natural resource management relies on adaptive management to address imprecise knowledge and to avoid the field's own version of "the twin traps of overtreatment and therapeutic nihilism" (e.g., the Hippocratic Oath, Edelstein 1943). The backbone of this approach is feedback among researchers, managers, and policy makers who together establish experimental treatments, quantify their efficacy, and direct resources. An analogous framework was not in place to address either chestnut blight or much of the management response to the decline of eastern hemlock populations. In the case of sudden oak death, an adaptive management approach is more likely to identify treatments which judiciously use limited management resources (Filipe et al. 2012) and avoid loss of genetic diversity (Hayden et al. 2011; Kjær et al. 2012) in comparison to reactive actions such as the attempt to construct a barrier to arrest the spread of chestnut blight (Freinkel 2007). The benefits of this approach are already very clear; one of the most important initial breakthroughs regarding sudden oak death was the discovery that *P. ramorum* was the cause of widespread oak and tanoak mortality (Rizzo et al. 2002) which laid to rest spurious hypotheses that the mortality was caused by insects or native pathogens. Adaptive management further relies on clear articulation of management objectives while also recognizing the need to evaluate treatments to achieve these objectives. The extent of the *P. ramorum* invasion suggests management goals must be comprehensive enough to match the magnitude of the disease and recognize technical and practical limitations in order to identify where, when, and in what combination available techniques will be most effective in slowing pathogen spread and maintaining the cultural and ecological value of tanoak.

TANOAK MORTALITY: PATTERNS AND IMPACTS

Tanoak has low timber value and the economic value is further lowered because of competition with commercial timber species, i.e., Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco (Harrington and Tappeiner 2009). Before the 1950s, tanoak-bark extracted tannins were important to California's leather industry, but the advent of synthetic tanning compounds has shifted the economic perspective on this tree (Alexander and Lee 2010; Bowcutt 2011). Prior to the emergence of sudden oak death, most recent research involving tanoak focused on quantifying and reducing competition with coniferous species central to commercial timber production often through the use of herbicides (Harrington and Tappeiner 2009; Bowcutt 2011). Little basic research has been conducted on tanoak and the measurement of growth characteristics, their relationship with disease resistance, and descrip-

tion of flora and fauna obligate to or associated with tanoak have only recently been undertaken (Bergemann and Garbelotto 2006; Cobb et al. 2012b; Wright and Dodd this volume). Although the risk of pathogen-driven, regional-scale removal of tanoak from the forest overstory is becoming increasingly clear, we face a critical lack of understanding as to what and how many species may be threatened by the widespread mortality of this common tree.

Even though *P. ramorum* has not yet invaded most of the tanoak range (Meentemeyer et al. 2011), the pathogen has significantly impacted tanoak from the Big Sur region (Monterey County, CA) north to Sonoma County, CA. In these regions, sudden oak death has caused widespread loss of overstory tanoak trees, significant shifts in overall forest composition, and outright extirpation of tanoak from some stands (Meentemeyer et al. 2008b; Ramage et al. 2011; Cobb et al. 2012b; Metz et al. 2012). These forests occur across topographically, environmentally, and biologically diverse landscapes where several different conifer and broad-leaved trees are likely to experience increases in density, biomass, and dominance as a result of the decline of tanoak populations. Metz et al. (2012) and Cobb et al. (2010) examined sudden oak death-impacted California stands ranging from relatively dry, mixed-evergreen forests to relatively cool and moist redwood-dominated forests; in both studies, tanoak mortality was associated with increased dominance of bay laurel. Given that *P. ramorum* establishment and disease emergence is associated with bay laurel abundance (Maloney et al. 2005; Meentemeyer et al. 2008a; Cobb et al. 2010), bay laurel is often situated to benefit from tanoak population decline. This shift in species composition has the additional impact of improving habitat for *P. ramorum*, suggesting that the pathogen will persist even if tanoak becomes locally extinct (Cobb et al. 2012b).

Additional shifts in species composition due to sudden oak death are also likely in North Coast forests from Mendocino County to Curry County, OR. While the current distribution and prevalence of *P. ramorum* in the North Coast is lower compared to the central coast where the pathogen was initially introduced (Fig. 1), pathogen invasion and associated tanoak mortality have mobilized management actions by state, private, and federal land managers (Rizzo et al. 2005; Valachovic et al. 2008; Goheen et al. 2009). In North Coast forests, Douglas-fir and redwood (*Sequoia sempervirens* [Lamb. ex D. Don] Endl.) have greater importance in terms of density, biomass, and basis in local economies; these characteristics are likely to favor an increase in dominance by these species in areas following tanoak mortality. Notably, forests in Del Norte

County, CA and Curry County, OR are notable for their lower abundance of bay laurel especially compared to forests in the central coast, especially Big Sur (Monterey County) and Sonoma County (Lamsal et al. 2011). *Phytophthora ramorum* is likely to invade and cause disease even when tanoak is the sole sporulation-supporting species (Rizzo et al. 2005; Goheen et al. 2009; Meentemeyer et al. 2011) although mortality rates are likely to eventually slow because of a negative feedback on pathogen populations when hosts die (Cobb et al. 2012b). Additionally, pathogen-killed trees or cut tanoak often develop prolific basal sprouts (Harrington and Tappeiner 2009; Cobb et al. 2010; Ramage et al. 2011), which may be sufficient to perpetuate pathogen populations and maintain spread in stands that do not include bay laurel (Cobb et al. 2012b).

Sudden oak death also has far-reaching economic, cultural, and ecological impacts. Spread of *P. ramorum* via ornamental nursery plants was responsible for the initial introduction to California and continues to play a role in spread within the United States and internationally (Garbelotto and Hayden 2012; Grünwald et al. 2012). Regulation of nursery stock, a costly but necessary management action, has been initiated to address this pathway of pathogen spread (see also Alexander and Lee 2010). For individual property owners, the loss of oak and tanoak directly impacts property values (Kovacs et al. 2011), and increased disease-caused fuel loadings at wildland-urban interfaces could augment the risk of property loss during wildfire (Metz et al. 2011; Valachovic et al. 2011). Similarly to American chestnut, tanoak has historically been an important component of human nutrition and local culture; tanoak resources retain significant cultural importance to many Native American communities in California (Bowcutt 2011). From a functional ecology perspective, tanoak is the sole ectomycorrhizal host in many forests (Rizzo et al. 2005) and supports ectomycorrhizal diversity on par with *Quercus* species (Bergemann and Garbelotto 2006). Tanoak-wildlife associations are poorly described, but the large nutritious acorns are likely used by many species and a recently described insect pollination pathway suggests yet undocumented insect communities and ecological interactions that may be impacted by the loss of tanoak (Wright and Dodd this volume).

DISEASE TREATMENTS: MODELS AND EXPERIMENTS

A central problem of managing emergent pathogens is that the available biological or epidemiological understanding is usually insufficient to control disease at the earliest stages of

outbreak. When epidemiological understanding is flawed, seemingly appropriate management actions may actually increase pathogen spread and disease intensity (Ndeffo Mabah and Gilligan 2010), or simply be insufficient to control pathogen spread despite large investments of management resources (Filipe et al. 2012). Research is essential to addressing these inefficiencies and maximizing the benefits of disease management. Epidemiological models can help guide management by estimating the efficacy of treatments and forecasting the spread and impacts of pathogens based on current data. Of equal importance are field experiments designed to test treatment efficacy and model structure. Field experiments are also essential in establishing a feedback among treatment application, monitoring, and research efforts, including modeling, which comprise adaptive management. For example, field studies improve the understanding of pathogen biology and epidemiology, which can be applied in models to identify the most appropriate treatments thus generating hypotheses that are testable with further field experiments (Snieszko 2006; Gilligan and van den Bosch 2008).

Models of disease risk based on host distribution, environmental conditions, and pathogen spread are useful tools for understanding where and when tanoak mortality will occur. The initial risk models for sudden oak death in California and Oregon (Meentemeyer et al. 2004; Václavík et al. 2010) identified locations that are optimal for pathogen establishment. These models have been reliable tools because the underlying epidemiological assumptions have subsequently been demonstrated to be biologically accurate (Meentemeyer et al. 2012). More recent models incorporate spread following establishment in a given set of locations (Meentemeyer et al. 2011; Filipe et al. 2012). These dynamical models enable estimation of a probable time of invasion for specific tanoak populations and suggest that the majority of the tanoak range is at risk of pathogen invasion and disease emergence over the next several decades. In conjunction with tanoak distribution models (Lamsal et al. 2011), these *P. ramorum* spread models hold promise to predict the timing of disease emergence, risk of tanoak population decline (Dillon et al. this volume), and changes in ecosystem functions such as carbon cycling (Cobb et al. 2012a). Further development of models and datasets to identify levels of biodiversity, cultural, or ecological value would be useful as an overlay with risk models (e.g., Meentemeyer et al. 2004; Václavík et al. 2010) to aid in identification of specific stands where resources for tanoak conservation should be focused.

Management of isolated outbreaks of *P. ramorum* has largely relied on removal of infected hosts to reduce inoculum. These treatments are often combined with removal of susceptible hosts

in the surrounding area in an attempt to account for undetected infections (treatment buffers) and have been implemented in southern Humboldt County, Redwood Valley (northern Humboldt County), and Curry County, OR (Hansen et al. 2008; Valachovic et al. 2008). These treatments, when done at an early disease stage, are clearly effective in reducing local pathogen prevalence and the likelihood of spread within treated stands (Hansen et al. 2008; Goheen et al. 2009), suggesting overall rates of spread in the landscape are slowed by aggressive and rapid interventions (Filipe et al. 2012). However, in each case the pathogen has not been eradicated by the treatments and spread throughout the landscape has continued. Undetected, or cryptic, infections are an important source of this continued spread into uninfected stands (Filipe et al. 2012). The broad *P. ramorum* host range, asymmetric impacts on hosts (some hosts support sporulation but are not killed by infections), cryptic infections, and survival in habitats such as soil and watercourses make eradication from a region exceedingly difficult (Hansen et al. 2008; Goheen et al. 2009). However, disease management need not attain 100% pathogen reduction to be effective. Slowing pathogen spread within the landscape is valuable, as it provides time to plan and proactively manage for ecosystem impacts, such as increased fuel loads, stress to biodiversity associated with tanoak, and the accompanying loss of acorn production.

As new isolated outbreaks emerge in northern California and southern Oregon it will become necessary to focus limited management resources to achieve specific cultural and biological conservation goals. Inoculum-reduction treatments such as attempts to locally eradicate the pathogen are expensive to apply and demand significant investments from land managers, researchers, and field staff (e.g., Valachovic et al. 2008) suggesting a shift from pathogen-centric to host-centric management will be more effective to reaching conservation goals when an individual outbreak reaches some yet undefined threshold. However, limiting spread into specific uninvaded landscapes will be aided by attempting eradication of isolated outbreaks as these treatments are likely to reduce inoculum (Filipe et al. 2012). For example, the Redwood Valley outbreak is strategically important given its proximity to culturally and ecologically valuable tanoak stands on tribal lands, within Redwood National Park, and an other nearby public and private lands with large tanoak populations. Pathogen-centric treatments in Redwood Valley have likely slowed *P. ramorum* spread into these valuable nearby areas by reducing inoculum loads. However, further removal of isolated infections outside of the treated area may be needed to attain maximum inoculum reduction or as part of

host-centric management that increases the resiliency of these tanoak populations and protects their associated biodiversity, ecological function, and cultural value. When to shift from pathogen-centric to host-centric management or identifying the optimal balance of each approach is an outstanding question for land managers working to address

P. ramorum and other forest disease outbreaks. Epidemiological models can inform both pathogen-centric and host-centric management actions (Fig. 2). Often, treatments for each management type will use the same techniques (stand thinning, infected host removal), but the timing and location of treatments may differ. Some insights into the design of these treatments can be gleaned from stand-level epidemiological models which often describe the amount of inoculum that can reach a given individual host through the concept of force of infection (FOI) (for examples, see Meentemeyer et al. 2011; Cobb et al 2012a; Filipe et al. 2012). FOI often has two components: the number of infected hosts weighted by a dispersal kernel (a function of relative distance between hosts), and the rate at which each infected individual transmits the pathogen to susceptible individuals. Sporulation rates vary across host species and are dependent on environmental conditions (rainfall, temperature), therefore formulations of FOI may include species specific pathogen spread factors as well as environmental variation. In addition, the length of time an individual remains infectious, known as the infectious period, also determines the number of individuals which spread a pathogen. Infectious period is poorly quantified for bay laurel and tanoak, but models demonstrate that this parameter can influence rates of pathogen spread at stand-to-landscape scales as well as the persistence of the pathogen within invaded stands (Cobb et al. 2012b; Filipe et al. 2012). The rate of spread and tanoak mortality within a population or landscape increases with FOI and management actions can be directed at one or more of its components. Therefore, the achievement of specific management goals will be improved by understanding which components of FOI are being acted upon by a given treatment. In general, eradication treatments reduce the number of hosts spreading the pathogen but do not change the rate of spread from each infected host. This is important because infected individuals that remain untreated support continued local and regional pathogen spread (Hansen et al. 2008; Filipe et al. 2012). Prophylactic chemical treatments, such as phosphonate injections, have been shown to reduce the susceptibility of individual tanoak against *P. ramorum* (Garbelotto and Schmidt 2009); while further research is needed on the efficacy, longevity, phytotoxicity and environmental interactions with phospho-

nate, in general protection of individual trees has been shown to be effective in slowing spread within some populations. Genetic variation within host species may also reduce susceptibility and subsequent pathogen spread. Bay laurel populations in Oregon (known locally as “myrtlewood”) are not as abundant, susceptible, and consequently not as important in spreading *P. ramorum* as they are in much of California (Hansen et al. 2005; Hüberli et al. 2011), suggesting genetically based differences among host populations may influence disease severity in different regions. Similarly, Hayden et al. (2010) found evidence of resistance to *P. ramorum* infection within tanoak populations, indicating that patterns of resistance could influence tanoak susceptibility or mortality within stands. Similarly to chemical protection treatments, further work is needed to understand how resistance influences pathogen spread rates. Recent modeling results suggest the degree to which management actions reduce *P. ramorum* infection rates can directly influence the number of tanoak that maintain an overstory canopy position in *P. ramorum* invaded forests (Fig. 3). Following a line of tested epidemiological models (Filipe and Gibson 2001; Gilligan and van den Bosch 2008; Ndeffo Mabah and Gilligan 2010; Filipe et al. 2012), Cobb et al. (2012a) developed a stand level model of disease outbreak with dynamic vegetation composition and tanoak size structure. These models demonstrate that a desired outcome of host-centric management may be feasible: retention of tanoak, including large tanoak, even though *P. ramorum* has invaded the stand. The model shows a critical level of tanoak density (tanoak stems ha⁻¹) below which the pathogen is not able to maintain spread from host to host and consequently, does not diminish tanoak populations or remove overstory tanoak. These results assume bay laurel is not present in, or has been removed from the stand and that remaining tanoak trees are evenly distributed across the stand. The models also suggest that slowed host-to-host infection rates result in better retention of the habitat and ecosystem function provided by tanoak (Fig. 2). Slower infection rates could be achieved by increasing tanoak resistance or stand-level application of effective chemical protection. However, identification of tanoak resistance prior to treatments is currently limited by the lack of molecular-resistance markers; this technical limitation must be overcome to use resistance measurements in broader-scale preemptive treatments. Regardless, the epidemic threshold predictions of the model (e.g., Fig. 3) should still be tested with field experiments, including current phosphonate applications (Garbelotto and Schmidt 2009) and tanoak thinning treatments to understand under which conditions these



FIG. 2. Landscapes and stands that have not been invaded by *Phytophthora ramorum* (A) offer different opportunities and require different management approaches compared to invaded forests (B) when the goal is to retain tanoak and its associated flora and fauna. Variation in the likelihood of pathogen invasion into pathogen-free landscapes and stands is largely driven by proximity to pathogen invaded stands and community composition. Community composition can be manipulated to slow invasion and disease impacts. Disease impacted stands (e.g., B) require a host-centric management approach that avoids removal of surviving tanoak, protects potential genetically based resistance, and retains ecological functions and species obligate to tanoak. In both cases, successful conservation of tanoak will require continuous feedback between research and management to establish baselines, test hypotheses, and determine the efficacy of management actions.

density thresholds are overcome through long-distance dispersal events (Filipe and Gibson 2001; Gilligan and van den Bosch 2008), sporulation from species not thought to be epidemiologically significant, or human-mediated transport of infected plants (Cobb et al. 2012b; Filipe et al. 2012).

MANAGEMENT GOALS DEFINED: CONSERVE BIODIVERSITY ASSOCIATED WITH TANOAK

Phytophthora ramorum has, and will continue to alter the distribution, prevalence, and biomass of tanoak across California and Oregon. A difficult reality of this disease is that much of this tanoak loss has and will occur regardless of the amount and efficacy of management actions. However, the available management tools and current understanding of the disease may be sufficient to avoid the worst possible outcomes such as the removal of large trees and consequent loss of ecological function (cf., Orwig 2002; Ellison et al. 2005). Management efficacy should

be measured at least in part by the success in retaining biodiversity and function associated with tanoak; retention of tanoak is likely to be easier in community or environmental conditions where pathogen spread is lower. Currently, many culturally and ecologically significant tanoak populations have yet to be invaded by *P. ramorum* (Lamsal et al. 2011; Meentemeyer et al. 2011), and timely actions have the potential to reduce future impacts of this disease.

Invaded Stands and Landscapes

Invasion status is a useful first distinction for management efforts and techniques as *P. ramorum* invasion of a stand eliminates the usefulness of many treatments (Fig. 2). For example, prophylactic treatments are ineffective on trees that are already infected (Garbelotto and Schmidt 2009). Similarly, limiting inoculum influx into stands where the pathogen is already established may have a minimal effect in reducing disease because most inoculum is produced

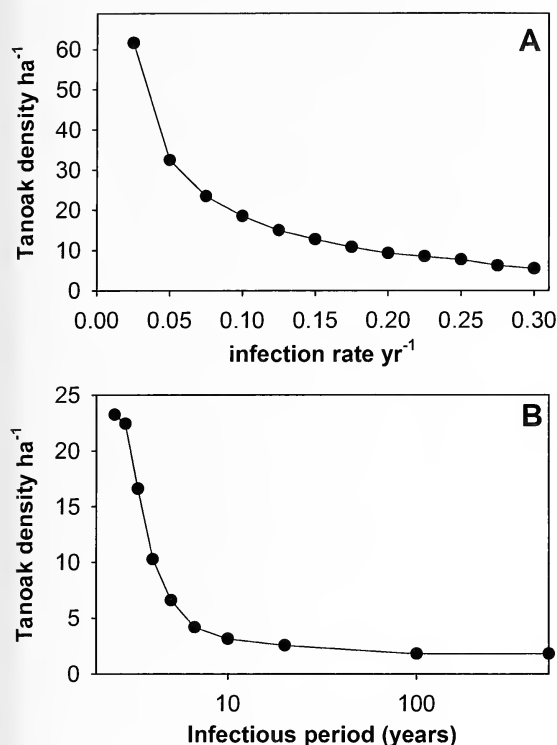


FIG. 3. The epidemiological characteristics of *Phytophthora ramorum* affect the threshold density of large tanoak trees (all trees > 30 cm diameter at 1.3 m) below which *P. ramorum* outbreak cannot be sustained in a parameterized epidemiological model (Cobb et al. 2012b). (A) The epidemic thresholds for tanoak density decreases with increasing infection rate. (B) Similarly, the density of large tanoak decreases with increasing infectious period (log scale; infection rate was kept constant at 0.3).

locally (Davidson et al. 2005; Mascheretti et al. 2008; Cobb et al. 2012b). *Phytophthora ramorum*-invaded stands are potential pathways of spread and the quarantine of infected, sporulation-supporting plants from these stands is a judicious action to reduce, though not eliminate, this pathway of long-distance pathogen spread.

Managers increasingly face isolated outbreaks that threaten to spread into the wider landscape. In Oregon, emphasis has been placed on monitoring and rapid implementation of eradication-type treatments within a designated quarantine zone (Hansen et al. 2008). In northern Humboldt County, the isolated outbreak in Redwood Valley was also addressed with a rapid eradication attempt response, but discovery of the pathogen outside of the treatment area raises the question of what follow-up treatments are needed to maximize the benefit of the initial intervention. The model designed by Filipe et al. (2012) was used to examine a number of landscape-level treatments including inoculum-reduction treat-

ments (such as eradication attempts) at the initial invasion or preemptive host removal ahead of the infection, and construction of a host-free barrier at the landscape-scale. Among these treatments, preemptive removal of hosts ahead of the initial invasion and removal of infected hosts at the initial invasion, similar to

the strategy in Oregon, were found to be most effective in slowing *P. ramorum* spread as long as the treatments were applied early during the epidemic and the scale of treatments matched the scale of the invaded area. The landscape-barrier treatments were not effective in slowing the spread or protecting particular areas because continued spread from undetected infections, or long-distance dispersal across the barrier overcame these treatments.

In regions with the most extensive *P. ramorum* invasion, eradication attempts are a poor choice of management. In highly invaded stands from Big Sur to Sonoma County, *P. ramorum* populations are so large and widely established that any benefit from local removal of infected trees would be overcome by reinvasion from adjacent stands. Eradication attempts always represent a tradeoff between causing tree mortality through cutting and herbicides vs. allowing the pathogen to cause tree mortality. In highly invaded landscapes, management should be aimed at reducing disease impacts and protecting high-value individual stands or trees. For example, in the fire-prone Big Sur landscape, high-density tanoak stands are problematic because sudden oak death generates significant amounts of dead fuels (Metz et al. 2011; Cobb et al. 2012a). Stands with accumulated dead fuels also suffered greater amounts of soil damage during the 2008 Basin Fire (Metz et al. 2011; Big Sur). These patterns suggest treatments which increase resiliency of tanoak populations to *P. ramorum* while also reducing dead fuels may have substantial benefits in terms of reducing ecological costs caused by wildfire in disease impacted forests. Disease-generated fuels are dependent on the rate of mortality and the amount of tanoak biomass present before invasion. This suggests preemptive reduction of tanoak density combined with bay laurel removal is likely to slow disease-driven dead fuel accumulation and reduce maximum amounts (Valachovic et al. 2011; Cobb et al. 2012a). These treatments could easily be structured to retain specific trees such as larger or more resistant individuals and increase spacing between individual trees in order to reduce within-stand spread. However, the effects of increasing stand openness are unresolved; pathogen dispersal may be less impeded in more open stands or, conversely, microclimate conditions could be less suitable to sporulation and infection (Rizzo et al. 2005). This uncertainty reflects the need for further experimental treatments to

understand the interactions of management actions with the epidemiology of *P. ramorum*. The Big Sur region is a strong candidate for experimental fuel and disease reduction treatments given the frequency of fire and the extent of sudden oak death in this region (Rizzo et al. 2005; Meentemeyer et al. 2008b; Metz et al. 2011).

Uninvaded Stands and Landscapes

The most effective strategy to prevent impacts of sudden oak death is to prevent *P. ramorum* invasions into new, at risk environments altogether. However, the history of *P. ramorum* is notable for numerous and often surprising invasions (Werres et al. 2001; Rizzo et al. 2005; Hansen et al. 2008; Brasier and Webber 2010) and current models suggest many stands and landscapes will be invaded in the coming decades (Meentemeyer et al. 2011). Proactive management of uninvaded stands may be much easier to implement where manipulation of stand and community structure are already planned to achieve management goals apart from disease. Where ever possible, host-centric management should aim to achieve multiple goals (Fig. 2).

The design, implementation, and evaluation of preemptive disease treatments are difficult from a research perspective because invasion dynamics are idiosyncratic. Without pathogen invasion of a stand—which is never guaranteed—the efficacy of a preemptive treatment cannot be evaluated. At the same time, intentional pathogen introduction to uninvaded areas must be ruled out on ethical grounds. We suggest two actions that help overcome this practical problem. First, disease management should be put in the context of long-term management goals, such as the reduction of fuel loads, growth of timber species, desired community composition or canopy structure, and/or enhancement of biodiversity. Second, further effort should be allocated to developing models for management evaluation. Models provide insight into the consequences of landscape-level management when experiments at this spatial and/or temporal scale are not possible (Meentemeyer et al. 2012). Lastly, to implement treatments for emerging outbreaks, we caution that management goals must be consistent with the priorities and level of cooperation within the local community (Alexander and Lee 2010).

Genetically-Based Resistance

Genetically-based resistance to *P. ramorum* in tanoak has the potential to be of great practical value. Stands with greater innate resistance are likely to experience lower rates of pathogen spread, fewer disease impacts, and have larger

tanoak populations following challenge by *P. ramorum* (Fig. 3). In a study quantifying patterns of tanoak resistance, Hayden et al. (2010; 2011) found variation in susceptibility within tanoak populations, but fairly equivalent susceptibility among populations. If this pattern is broadly representative of tanoak genetic patterns, individual stands are unlikely to resist invasion by *P. ramorum* on the basis of genetic composition alone. However, resources from within stands could be used to maximize tanoak population resiliency in conjunction with other treatments, or to develop less susceptible tanoak growing stock suitable for restoration in *P. ramorum*-invaded areas and preemptive planting treatments in uninvaded landscapes. Further work is needed to increase the ease and rate of identifying tanoak resistance, to determine if rates of sporulation differ in less susceptible trees, and to develop tanoak suitable for restoration.

Where the management goal is to retain biodiversity and function associated with tanoak, treatments need not conserve every living tanoak. Rather, these treatments must retain tanoak populations large enough to maintain both the species and its valued ecological functions. Moreover, sampling and conservation efforts should be targeted to retain genetic diversity across regions of known tanoak differentiation. A genetic analysis of neutral markers by Nettel et al. (2009) has shown deep divisions in chloroplast markers between central coastal California tanoak populations and northern coastal-California/Klamath/Sierra tanoak populations, along with evidence of considerable pollen flow among populations. The variance structure in neutral nuclear genetic markers was similar to the variance in resistance measured on leaves cut from wild trees, with more variance within populations than there was among populations (Hayden et al. 2011). In pathogen-invaded landscapes, disease may be a useful force to select for more resistant tanoak. Hayden et al. (2011) suggested that greater prevalence of resistance at some sites could reflect a selection effect of the pathogen, and McPherson et al. (2010) reported the survival of several mature tanoaks after nearly a decade of monitoring in a *P. ramorum*-invaded forest. These results argue for retention of tanoak where *P. ramorum* has already killed a large portion of the tanoak population. In highly disease impacted stands, treatments which remove surviving trees would clearly exacerbate the loss of tanoak and may reduce genetic resources important for developing molecular markers of resistance and restoration planting stock.

Protect High Conservation Value Stands

Targeted conservation acquisitions, such as land purchases or conservation easements, are

often used to protect rare species or habitat and could be effective in some cases for retaining high-value tanoak populations, such as uniquely located or isolated stands threatened by development. For example, the most southern tanoak populations occur in Santa Barbara County in small and relatively high-elevation stands and a larger geographically-separated tanoak population occurs in the foothills of the central to northern Sierra Nevada range (Fig. 1). In both cases, these tanoak populations hold important genetic diversity, and have lower likelihood of *P. ramorum* invasion because of their isolation, poorer environmental conditions for pathogen sporulation, and low spread risk from adjacent stands (Nettel et al. 2009; Dodd et al. 2010; Meentemeyer et al. 2011). However easements can restrict available management tools needed to slow pathogen spread or protect individual trees and will not be appropriate for many sites or as a method to protect large tanoak populations.

CONCLUSIONS—GUIDELINES FOR
TANOAK CONSERVATION

The goal of tanoak conservation requires an adaptive management approach where management actions and research are designed and conducted with synergistic feedback. We suggest a set of overarching management and research guidelines to achieve this objective.

1. Define the management goals for *P. ramorum* and integrate tanoak conservation as part of a broader vision of landscape management melding treatments for fire, wildlife, aesthetics, and other stand-level goals.
2. Continue efforts to develop field, lab, and molecular tools to identify resistance to *P. ramorum* and develop methodologies to identify and map resistance in the field. Combine this information with stand-to-landscape level epidemiological models to identify tanoak stands with the greatest resiliency to disease.
3. Conduct field experiments to evaluate the efficacy of host-centric management treatments to retain tanoak in *P. ramorum* invaded stands. In combination, conduct epidemiological and bio-economic analysis to identify the optimal timing to shift from pathogen-centric management (eradication and similar slow-the-spread treatments) to host-centric management aimed at retaining tanoak in invaded lands.
4. In uninvaded stands or landscapes where tanoak is highly valued, increase the resiliency of these populations by reducing the potential for pathogen spread (i.e., reduce bay and tanoak densities) while retaining the most resistant tanoak individuals.

5. Develop host-centric, ameliorative and proactive treatments that reduce the ecological costs of disease for: fire prone forests, regions with the greatest potential ecological impact of disease (i.e., areas with high tanoak importance and biomass), and lands where tanoak has the greatest cultural value.
6. Work with the public to increase appreciation and interest in tanoak and to encourage further participation in pathogen monitoring and disease management (cf., Alexander and Lee 2010).
7. Increase collaboration among state and federal agencies, and public-private partnerships to support management in tanoak stands.
8. Expect the unexpected. *Phytophthora ramorum* is a remarkably well-adapted pathogen for which the native host or geographic range has not yet been identified. The importance of pathogen characteristics often becomes clear only after a new management problem has emerged.

ACKNOWLEDGMENTS

Katherine Hayden and Joao Filipe contributed to this paper as second authors. The authors are grateful for comments and criticism to a previous version of this paper from four anonymous reviewers. The paper has also been improved by discussions with H. Mehl, M. Metz, and B. Twieg. We thank C. DeLong for designing Fig. 1. This work was funded by NSF grant DEB EF-0622770 as part of the joint NSF-NIH Ecology of Infectious Disease program, the Gordon and Betty Moore Foundation, and the USDA Forest Service, Pacific Southwest Research Station. JANF and CAG were funded by DEFRA (United Kingdom) and USDA.

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